The breeding ecology and potential impacts of habitat change on the Malaysian plover *Charadrius peronii* in the Gulf of Thailand.

By

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B.Sc., University of Victoria, 2000
M.Sc., University of Oxford, 2002

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In the Department of Geography

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ABSTRACT

Anthropogenic habitat change is the most important factor contributing to global losses in biodiversity. Ecological research can help identify the mechanisms that cause these declines by relating environmental characteristics to wildlife habitat use and productivity. Such studies can contribute to the design of land-use practices that enhance wildlife populations in conservation areas and promote efficient compromises between human use and conservation.

The conflicts between human-use and conservation are particularly evident in coastal areas, which have enormous economic value and are thus coveted areas for development. Human-use can alter the habitat quality and affect coastal taxa, such as shorebirds.

In this study I examine the breeding ecology and conservation biology of a beach-nesting, near-threatened shorebird, the Malaysian plover *Charadrius peronii,* which breeds on coastal areas throughout Southeast Asia. Although nearly half of the threatened shorebird species breed in tropical areas, little research has been conducted on the conservation and ecology of these species. My study is the first detailed research conducted on the Malaysian plover. It contributes to a better understanding of the environmental factors constraining breeding strategies in the tropics and identifies key mechanisms linking anthropogenic habitat change and wildlife populations.

I used behavioural approaches to collect a wide range of data over a short-time period in order to describe the breeding ecology of Malaysian plovers, evaluate different types of constraints, identify anthropogenic impacts and provide recommendations on management approaches to mitigate the impacts of habitat change.

Malaysian plovers have long breeding seasons, high site fidelity, complete biparental care and can nest multiple times in a single year. In contrast to shorebirds in Arctic environments, where fecundity is limited by the brief pulses of high seasonal productivity, Malaysian plover fecundity appeared to be constrained more by habitat availability rather than time. Malaysian plovers began defending territories several months prior to the breeding seasons and nested in the same habitats even if there were significant reductions in habitat quality throughout the course of the breeding season.

In the Gulf of Thailand tourism-related habitat change that narrows beaches, alters vegetation structure and enhances human disturbance levels reduce habitat availability and breeding success. Enhanced vulnerability of clutches to tidal flooding, chicks to predation, exposure of eggs to heat and chicks to predation may be key mechanisms leading to these effects. Moreover Malaysian plovers had a density-dependent decline in breeding success. Consequently, if birds are displaced from preferred beaches due to habitat change, then breeding success may be reduced in otherwise high quality habitat as plovers crowd into remaining beaches.

When people approach nesting or chick-rearing plovers, one or both of the adults will leave the clutch or chicks to conduct distraction displays. Compared to holarctic species, tropical shorebirds may be more vulnerable to the fitness impacts of human disturbance because even short periods of exposure to direct sunlight can cause clutch failure, whereas eggs are resistant to chilling. These results suggest that the environmental and ecological conditions in tropical regions may affect the susceptibility of breeding shorebirds to fitness impacts of anthropogenic disturbance and habitat change.

Future research should assess cumulative impacts of habitat change by conducting multispecies studies and include wintering or stopover shorebirds. As my research was conducted in the best Malaysian plover breeding habitat in Thailand, it is important to assess the generality of my results by comparisons to other regions or across several years in which there may be a different range of predators or prey. Finally, it is important to note that these types of ecological conservation studies are only a first step towards

successful protection of threatened species. The greater challenge is to tackle the ultimate socio-economic and institutional factors that limit the effectiveness of protected areas and contribute to the number of environmentally destructive coastal development projects.

TABLE OF CONTENTS

List of Tables

List of Figures

List of Equations

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DEDICATION

This dissertation is dedicated to Charoen Wataksorn, a fisherman, environmental activist, and a community leader who was murdered just outside his village in Bonok on 14 June 2004. Charoen died giving a voice to the whales, Malaysian plovers, fish and small-scale rural fishers whose needs are so often quashed by the rich, corrupt and powerful. Through his passion, courage, incredible resourcefulness and quick smile he inspired his community, and others and successfully halted the construction of a coal power plant on one of the beaches where I conducted my research. For me, Charoen and his wife Kornuma Pongnoi (Grarook), welcomed me into their community, gave me a place to stay, kept me fed, drove me around, spent endless hours with me at the police station, taught me to cook curries, bought me my quail eggs and helped me find my little birdies. I leave Thailand humbled, having given so little back to their cause in return, knowing that no amount of top quality conservation research that I conducted in Thailand could ever come close to accomplishing even a fraction of what could've been gained if Charoen had been allowed to live.

GENERAL INTRODUCTION

Expanding per capita consumption and human populations are causing rapid rates of species extinctions (Pimm et al., 2001). To mitigate biodiversity losses, there is a need to understand better the nature of the conflicts between people and wildlife. Conservation scientists can demonstrate causal pathways between anthropogenic change and wildlife population declines (Goss-Custard et al., 1995), describe habitat requirements for species, identify vulnerable species and ecosystems and help prioritise regions for conservation (Rodrigues et al., 2004; Eaton et al., 2005). Such studies can provide science-based recommendations to modify human behaviour in a way that helps enhance or maintain wildlife populations (Soule, 1985; Hunter, 2002).

Behavioural ecology

Within the expanding field of conservation sciences I have used a behavioural ecological approach for my dissertation. Behavioural ecologists use an evolutionary perspective to model how animals respond to environmental conditions in order to maximise fitness (Krebs and Davies, 1991). In the past decade there has been increased interest in the application of behavioural principles to conservation problems, and in particular to understand the potential fitness impacts of habitat loss or degradation (Gosling and Sutherland, 2000).

Habitat change is currently the leading cause of decline in global biodiversity (Newton, 1996; Lovejoy, 2002). The ability to predict population consequences of habitat change can help assess impacts of future development projects, or the potential benefits of different habitat restoration or management options (Goss-Custard et al., 1995; Sutherland and Norris, 2002). However, it is difficult to predict the impacts of environmental change on populations using traditional demographic approaches (Newton, 1995) because of the paucity of long-term population data for the numerous threatened species throughout the world (Sutherland and Norris, 2002). In addition, stochastic effects can often mask overall population trends (Ludwig et al., 1993; Saether and Engen, 2002) and key demographic variables such as fecundity may change in novel environments and at different population sizes (Dolman and Sutherland, 1995; Sutherland, 1998a; West et al., 2002).

Behavioural ecologists use simplified models in order to predict the responses of animals to changes in environmental conditions. When habitat is removed, altered or restored, individuals may choose different habitats to maximise fitness in the novel environment. These changes alter breeding or foraging densities and can affect survival or productivity in a density-dependent manner. Population changes can be modeled based on the fitness consequences of each of these individual decisions (Krebs and Davies, 1987; Sutherland and Anderson, 1993) and density-dependence functions (Pettifor et al., 2000). In this way, behavioural studies provide insight on the mechanisms that cause the observed changes in populations. Resource managers can then make us of these mechanisms in order to increase productivity or survival of wildlife.

Compared to traditional demographic or ecological studies, the results of behavioural studies are more easily applied to a wider range of environmental conditions, across different study areas, times or even species (Wiens et al., 1993; Sutherland, 1998b). This is because theories predicting the behaviour of individuals based on the assumption that they will always attempt to maximise fitness, will remain valid even if environmental conditions change (Stillman et al., 2000). In addition, behavioural parameters such as territoriality, foraging rates or habitat choice can be assessed over a relatively short time scale at lower costs and may allow for conservation measures to be implemented before populations show significant signs of decline (Sutherland and Norris, 2002). Consequently, they may be a particularly important area of research in developing countries where rates of biodiversity loss are particularly high and where there are scarce funds for ecological research and few long-term datasets.

Why geography?

Geographers seek to describe and explain spatial patterns and then use this knowledge to solve problems (Waugh, 2000). Although many aspects of this research could have been conducted in a biological sciences department, a key emphasis of this study was how environmental factors including human activities, varied across space and influenced shorebird habitat selection and constraints on breeding. Understanding interactions between the natural environment and human activities is a core theme in geographical studies (Waugh, 2000). Behavioural ecology was used to explain animal spatial patterns. However the goal of this study was an integrated and applied environmental geographical question that sought to provide recommendations on how to mitigate the conflicts between human use and biodiversity conservation.

Shorebird conservation

Currently nearly half of the global shorebird (*Charadriidae* and *Scolopacidae*) populations show signs of decline and habitat loss is thought to be a contributing factor (Senner and Howe, 1984; Myers et al., 1987; Piersma and Baker, 2000; International Wader Study Group, 2003; IUCN, 2006). Shorebirds are particularly vulnerable to anthropogenic habitat change because they are ecologically specialized and rely on coastal habitats such as wetlands, mudflats and beaches that have tremendous economic and subsistence values for people. These habitats are rapidly being replaced by urban development, aquaculture, tourism infrastructure and roads (Myers et al., 1987; Davidson and Rothwell, 1993; Clark, 1997). Coastal development (Senner and Howe 1984) can affect important foraging and breeding habitats for shorebirds by causing habitat loss (Lambeck 1991; Goss-Custard *et al.* 1995), a reduction in habitat quality (Sutherland 1998) or increased human disturbance (Pfister *et al.* 1992; Hill *et al.* 1997; Madsen 1998; West *et al.* 2002).

The conservation and monitoring of shorebirds can also be logistically difficult because shorebirds are highly mobile and utilize many different habitats, sometimes over different continents in a single year (Piersma and Baker, 2000). For this reason, it is difficult for managers to identify population bottlenecks, and also measure the fitness consequences of local habitat change (Sutherland, 1998a). Conservation of such migratory species requires collaboration across several disciplines and countries which can represent a tremendous challenge for resource managers.

Southeast Asia and Thailand

Almost 80% of the human population in Southeast Asia lives within 100 km of the coast (World Resources Institute, 2004). As these countries continue to recover from the 1997 Asian financial crisis, they now include some of the world's fastest growing economies and human densities. As a consequence there is a tremendous amount of pressure for subsistent human use and recreational development in coastal areas. Southeast Asia is also a region of high biodiversity and several areas are included as biodiversity hotspots for conservation or areas of endemism in almost all conservation prioritisation assessments (Myers et al., 2000; Rodrigues et al., 2004). Despite the potential for significant threats to biodiversity, remarkably little conservation related field research has been conducted in this region (Sodhi and Liow, 2000; Milton, 2003).

Within Thailand there are 541 red-listed species, including 113 endangered or critically endangered species. This can be compared to the mere 179 red-listed species that exist in Canada, a country with approximately 200 times the total land mass (IUCN 2006). Thailand's 2700 km coastline provides productive mudflats, saltpans and aquaculture ponds (Velasquez and Hockey, 1992) that are foraging habitats for 61 species of wintering or staging birds in the East-Australasian flyway (Robson 2002). This flyway supports 4 – 6 million shorebirds annually and has the largest number of threatened shorebirds out of any of the global flyways and includes species such as the Asian dowitcher (*Limnodromus semipalmatus*) and Nordmann's greenshank (*Tringa guttifer*) (Pedersen et al. 1996). In addition to use by migratory species, several resident shorebirds, such as the Malaysian plover and black-winged stilt (*Himantopus himantopus*) breed on beaches (Round *pers. comm.* 2003).

Although there have been numerous detailed shorebird conservation and ecology studies in temperate environments (Goss-Custard et al., 1995; West et al., 2002; Ydenberg et al., 2002) even basic information on habitat use, population size or species composition does not exist for shorebirds in Southeast Asia or in most tropical environments (Milton, 2003). This is a concern because nearly half of the threatened shorebirds breed in tropical habitats (IUCN, 2006). At present most of the evolutionary ecological theories addressing breeding ecology of shorebirds have been based only on research conducted in holarctic environments. It is crucial to conduct more research on tropical shorebird breeding ecology because dissimilarities in abiotic or biotic conditions between tropical and holarctic areas may affect natural constraints on breeding and populations (Martin, 1996). Such differences, may in turn, affect the type, extent and mechanisms of anthropogenic impacts.

Goals and Objectives

My study species is a small, beach-nesting, sedentary shorebird, the Malaysian plover *Charadrius peronii,* that nests on beaches throughout Southeast Asia (Robson, 2002). This species is near-threatened with a population of 10,000 and so far there have been no detailed published studies on the ecology, conservation or habitat requirements of the Malaysian plovers (IUCN, 2006) .

The primary objectives of this study are to examine the behavioural ecology and spatial patterns of habitat use in Malaysian plovers to understand and quantify the potential impacts of beach development on productivity. Second, this study will evaluate whether there could be any differences in vulnerability to anthropogenic change between under-studied tropical shorebirds and well-studied holarctic species. By addressing these objectives, I hope to provide recommendations on management approaches to reduce human impacts on Malaysian plover breeding populations in the Inner Gulf of Thailand and also highlight areas for conservation research that are particularly important for tropical nesting shorebirds.

Structure of dissertation

The dissertation is organized into two parts. The first part of my study is comprised of three chapters and will examine the breeding ecology of the Malaysian plover. The second part includes three chapters that focus on the conservation biology of the Malaysian plover and the potential impacts of habitat change.

The first chapter describes parental sex-roles of Malaysian plovers. In shorebirds, parental care strategies vary tremendously both among species and within species in different types of environment (Reynolds and Székely, 1997; Székely and Cuthill, 1999). This research identifies environmental factors that may influence breeding and constrain productivity of tropical shorebirds. Chapter one provides the back-ground for chapters two and three, in which I examine the Malaysian plover's ability to renest multiple times in one year. This research is important for understanding population constraints and the potential impacts of habit destruction or the value of restoration. If shorebirds are able to nest several times in a year without adversely affecting reproductive potential in future years, they may be more able to buffer human-induced reductions in breeding success (Haig, 1987; Winton et al., 2000; Weston and Elgar, 2005a).

The research on breeding ecology that I explore in part one provides the background to assess how anthropogenic factors affect the intensity of natural breeding constraints and affect productivity in part two of the dissertation. In chapter four, I combine behavioural observations, nest monitoring and develop habitat models to evaluate how changes in habitat structure due to tourism development and human disturbance could affect the amount of available habitat and breeding success for Malaysian plovers. In chapter five, I conduct a quantitative analysis of the factors that influence the time for a Malaysian plover to return to a nest after a disturbance. This study identifies the constraints that affect return times, and assesses whether behavioural responses to a disturbances can be used to assess potential fitness impacts of disturbance. In the final chapter I examine the use of salt flats as supplementary habitat for nesting birds and assess the potential for restoration and naturalisation of former aquaculture ponds and salt flats to buffer the impacts of beach habitat loss.

The dissertation concludes with a summary chapter synthesizing the findings, assessing the limitations of my research and whether I was able to meet stated objectives and making suggestions for future studies.

PART 1: BREEDING ECOLOGY

I. Parental sex-roles of Malaysian plovers during territory acquisition, incubation and brood care

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Abstract

In shorebirds, there is a tremendous variability in parental care strategies between species, populations and environments. Although numerous studies have examined parental care strategies in holarctic shorebirds, very little research has been conducted in the tropics. Here I examined diurnal parental sex-roles during territorial defence, incubation and chick-rearing in Malaysian plovers *Charadrius peronii* in the Gulf of Thailand. The costs and gains of particular parental behaviour may vary between the sexes and can be affected by environmental factors and chick age differently. Thus I also examined how temperature, prey availability, chick or embryo age and time of day influenced sex roles. During the daytime males spent more time defending territories and were further away from chicks, while females spent more time incubating eggs. Both adults contributed to chick defence during disturbances throughout the entire chick-rearing period. Total nest attendance (sum of both sexes) was influenced by only the modelled temperature of an unincubated egg. Prey availability, embryo age and time of day had no effect on total nest attendance. Males adjusted incubation effort in response to temperature only at high temperatures (>36 C^0) whereas females adjusted nest attendance at high and low temperatures. Chick age had no effect on the proportion of time adults spent defending territories or responding to disturbance. Pairs were more likely to fledge chicks if both the male and female spent more time defending territories. For Malaysian plovers, a high degree of cooperation between the sexes during parental care may help in

obtaining high quality breeding territories, maintaining body conditions during hot days, protecting offspring from predators and attacking conspecifics, and contribute to greater lifetime reproductive success.

Introduction

In shorebirds, parental care can vary among and within species, from equally shared biparental care to uniparental care by either the male or female (sub-order *Charadrii*). Due to this diversity, shorebirds have been used as model taxa to examine how selective pressures relating to the physical or social environment shape parental sex roles (Reynolds and Székely, 1997; Székely et al., 2006).

Animals adjust parental investment based on a trade-off between current and future reproductive success (Clutton-Brock, 1991). Sexual differences in parental care may occur because the fitness costs and benefits of territory defence, incubation or brood-care can differ between sexes (Brunton, 1988; Clutton-Brock, 1991). One of the key features causing sex-based differences in behaviour for birds is that females must attain energy and calcium reserves to lay eggs (Breitwisch, 1989; Székely and Lessells, 1993). Consequently females may reduce parental effort during periods when they are energetically constrained and could jeopardize future breeding success such as during or immediately after egg-laying, or in the last week of chick-rearing (Székely and Williams, 1995). Energetic factors may be particularly important in influencing female parental care for species that nest multiple times during a breeding season, have short inter-clutch intervals or undergo a costly migration immediately after breeding (Graul, 1976; Sandercock et al., 1999). Female shorebirds in highly productive environments may contribute more to parental care throughout the breeding season because they can more easily obtain the energy reserves necessary for egg production (Amat et al., 2000; Wallander and Andersson, 2003).

Although males do not incur egg-laying costs, they expend significant resources defending territories (Burger, 1981). Territory defence can improve breeding success by protecting resources, decreasing infanticide and also attracting potential mates (Dubois et al., 1998). In addition to these benefits that are shared between the mates, males may gain more from defending territories than females because by preventing other males from entering territories males may reduce the risk of cuckoldry (Nol, 1985; Zharikov and Nol, 2000). Consequently, except in territorial non-polyandrous shorebirds, males may spend more time defending territories than females and particularly prior to egg-laying when females are fertile (Brunton, 1988).

Virtually all of the research on how environmental, ecological or social conditions affect wader breeding strategies and paternal care has been conducted in temperate or arctic environments (Thomas et al., 2003a; Moreno, 2004). Very little is known about the ecology of any of the 32 plover species that breed mainly in the tropics. The longer breeding seasons, stable weather conditions, high and diverse predation pressures and shorter migration routes of most tropical species (Martin, 1996; Moreno, 2004; Weatherhead and Blouin-Demers, 2004) are likely to influence parental behaviour. More studies on parental care in tropical species are needed to describe parental behaviour and also identify factors that shape avian breeding ecology in a wider range of environmental or ecological conditions.

Here I describe the parental care patterns of Malaysian plovers *Charadrius peronii*, a near-threatened, beach-nesting shorebird breeding on beaches and wetlands in the Gulf of Thailand. I monitored plovers from November to July and compared territorial effort, nest attendance, chick defence and vigilance, and feeding rates between the sexes. Aside from an anecdotal note (Gregory-Smith, 1998) and general distribution information (Collar et al., 1999; Smythies and Davison, 1999; Robson, 2002), there are few detailed, published studies on this species (Yasué and Dearden, 2006a; Yasué and Dearden, 2006b; Yasué and Dearden, 2006c). The Malaysian plovers is an ideal species to explore some of the possible differences in parental sex roles between temperate and tropical areas because there are several well-studied temperate populations of closely related species such as the common ringed plover (*Charadrius hiaticula*), and temperate populations of Kentish plovers (*Charadrius alexandrinus*) (Purdue, 1976; Fraga and Amat, 1996; Wallander, 2003).

Within a population, many factors can alter the parental investment trade-offs (Székely and Williams, 1995; Székely and Cuthill, 1999) and lead to changes in the parental care roles. In this study I also examined whether temperature, prey availability and chick age had different effects on parental care behaviour of males and females. This part of my study provides a finer degree of resolution on the partitioning of parental care and helps to evaluate how environmental constraints and parental investment decisions shape breeding strategies.

As ambient temperatures rise above optimum incubation temperatures (35 – 37 ^{0}C) (Webb, 1987), one or both adults will increase nest attendance because exposed clutches become more vulnerable to heat-induced mortality (Dunning and Bowers, 1990; Weston and Elgar, 2005b; Yasué and Dearden, 2006b). Heat stress may also inflict greater costs to body conditions of incubating parent (Carey, 1980; Conway and Martin, 2000). Prey density could also affect nest attendance because plovers in territories with low prey availability may spend less time incubating nests and more time feeding (Erckmann, 1983).

The change in male or female nest attendance due to these environmental conditions depends partly on mate fidelity for future breeding attempts and paternal certainty. For species with high mate fidelity and generally low rates of extra-pair copulations (EPCs) the cost of nest failure is more similar between mates (Reynolds, 1996) and pairs may cooperate so that they can maintain pair bonds and breed successfully over several years with the same mate (Pierce and Lifjeld, 1998; Wallander et al., 2001; Blomqvist et al., 2002). In these types of breeding systems, if females have difficulties recovering body condition after laying eggs, males may be more likely to increase nest attendance during stressful periods and also contribute more to nest attendance in areas with low prey availability compared to females.

Alternatively, for species with lower mate fidelity or if one of the mates are able to renest with a different mate in a season, then there could be conflicts between the sexes on the value of the current brood and the appropriate amount of parental investment (Slagsvold et al., 1995; Ackerman and Eadie, 2003). In these types of breeding systems, the cost of current nest failure could be greater for females because of higher parental certainty (Westneat and Sargent, 1996). For this reason, female Malaysian plovers may be more likely to increase nest attendance during periods of heat stress or in environments with low prey availability.

Methods

Study area

All data were collected on beaches between Bornok village (99^0 53′ 12^0 00′), in Prachuap Khiri Khan and Laem Phak Bia village (100^0 05′ 13^0 03′) in Petchburi province in the Gulf of Thailand between 20 Nov 2003 - 25 July 2004 and 10 Jan – 28 July 2005 (

Figure I-1). In this region, there is a hot, humid and sunny summer from April to May (diurnal 28 - 42 ^{o}C) and a cloudier rainy season from June to July (diurnal 26 - 38 ^{o}C).

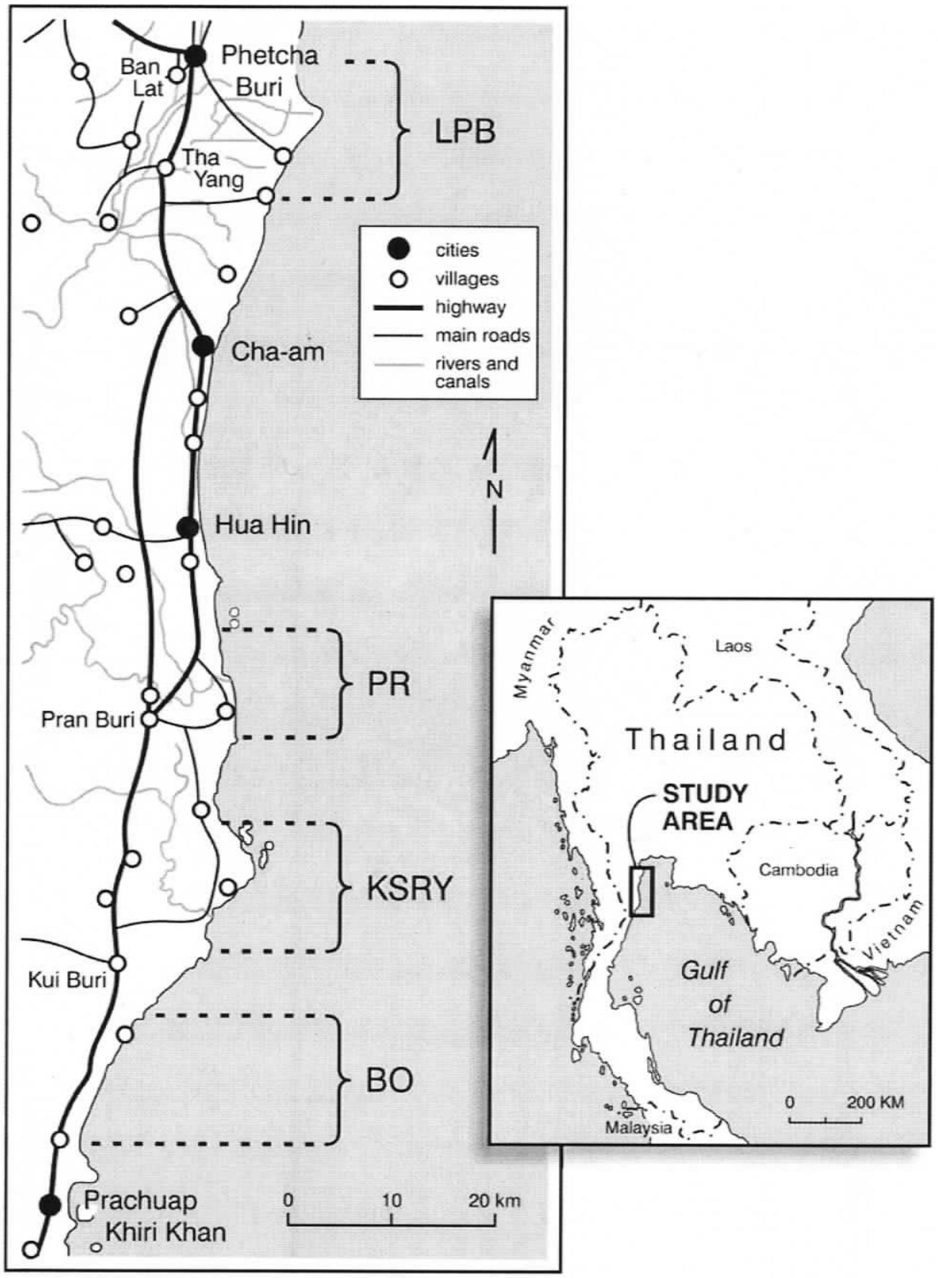

Figure I-1 Map of study area.

LPB = Laem Phak Bia, PR = Pranburi, KSRY = Khao Sam Roi Yod National Park, BO = Bornok.

Nest monitoring

Malaysian plovers defend 100 – 300 m long, multi-purpose rectangular territories that include an intertidal mudflat foraging area, a sandy beach for nesting and a shrubby vegetated area behind the beach that provide cover for chicks during disturbances (Yasué and Dearden, 2006c). Beginning in April, they lay two to three cryptic eggs in shallow scrapes. The eggs in a clutch hatch over one to three days after a 30 day incubation period. The chicks are precocial, never fed by parents, and fledge after 27 to 35 days (Yasué and Dearden, 2006a; Yasué and Dearden, 2006b; Yasué and Dearden, 2006c).

During the breeding season I found nests by searching in areas where pairs were frequently observed or by watching birds return to nests. I used a Garmin 60 GPS unit to record nest locations. Eggs were floated regularly to detect embryo mortality, estimate lay and hatch date, based on a 30 day incubation period (Yasué and Dearden, 2006a; Yasué and Dearden, 2006c)[Appendix 2]. I checked the nests every three to five days to determine nest survival or cause of failure. All eggs were weighed using a 10 g spring balance Pesola scale. Most adults were caught and banded either during the preceding winter (only in 2003/2004), summer or on nests using noose mats (Mehl et al., 2003) or funnel traps (number of banded adults/chicks 2004 and 2005: 118/88, 75/103). I captured and individually colour-banded chicks within two weeks of hatch and returned to the nesting territories weekly to assess chick survival up to 30 days. I did not conduct behavioural observations on birds that were caught on that same day.

In total, 86 and 126 nesting attempts of 54 and 79 pairs were monitored in 2004 and 2005. Family groups could be identified because at least one of the chicks or adults was individually colour-banded. It was possible to accurately assess fledgling success because broods did not move more than 300 m from nest sites. There were 80 banded breeding birds at the end of the field season in 2004 and 42 returned to breed within the study area in 2005.

1) Sex ratios in wintering flocks

In the non-breeding season, Malaysian plovers roost in tight flocks on wide beach sections at high tide. Although these winter flocks are likely to have several purposes such as reduced predation risk (Cresswell, 1994b) or mate selection, birds in these flocks also began defining territories and would frequently stop roosting to display or fight amongst each other. Thus sex biases in these flocks could indicate differential effort in breeding territory acquisition or unequal sex ratios (Székely et al., 2006). I counted the total number of males and females in these winter flocks based on obvious plumage differences (Robson, 2002) to determine whether there may be any difference between the sexes in pre-breeding site occupancy effort. Males have black crown, eye and chest bands and more extensive cinnamon on their head compared to females (Robson, 2002). 139 counts for flocks with more than five individuals were conducted in five different locations and days between November 2003 to March of 2004 and January to March 2005. If the same location was sampled more than once during a day, mean values were calculated. These five locations were at least 6 km apart and based on observations of banded individuals, adults plovers did not move between these locations. Thus I could assume that these sampling sites were independent from each other. I calculated mean values of the number of males and females per location.

2) Nest attendance and incubation

I watched incubating plovers using a 15 – 45 X spotting scope and 10 X 50 binoculars for a total of 163 hours from either a hide or a seated position on the mudflat located more than 150 m from the plovers. Nest observations lasted 1 to 2 hours (mean length = 75.7 ± 2.3 minutes; All measures of dispersion here and throughout text and figures are standard errors) and were conducted on 113 different nests (of at least 82 known colour-banded pairs [up to 95]) between April and July in 2004 and 2005. The duration of the nest observations depended partly on the incubation bout length. I ensured that in all observations in which adults visited the nest at least once, I was able to record at least one complete incubation bout that was not disturbed by the observer. The length of incubation bouts is shorter than temperate or Arctic species Malaysian plovers probably because heat stress forced the adults off of nests.

During nest observations I recorded the start and end times of incubation bouts. *Total nest attendance* was the percent of time during a nest observation in which either the male or female incubated the eggs. Male and female attendance refers to the proportion of the nest observation in which each of sex attended nests.

Egg temperature model

I modelled the egg temperature of an unshaded clutch from measurements of shaded air temperature, cloud cover and time of day that I measured during incubation observations. I developed the exposed egg temperature model by measuring the temperature inside quail eggs (*Coturnix coturnix)* that are a similar size and pigmentation to Malaysian plover eggs in recently abandoned Malaysian plover nest cups on 42 different occasions. For a detailed description of the methods used to develop the model see Yasué and Dearden 2006b (Appendix 1).

Prey availability

Small *Scopimera* (bubbler) crabs are a major prey type for Malaysian plovers (Yasué and Dearden, 2006c). I measured prey availability along a 200 m long intertidal mudflat section parallel to the beach in front of each Malaysian plover nest. At each mudflat sampling section I measured the width of the mudflat (perpendicular to the beach) where crab burrows were present. I paced the mudflat and visually estimated the proportion of the area with high (>100 m^{-1}), medium (20 – 100 m^{-1}) or low crab densities (< 20 m^{-1}). These proportions were used to calculate weighted average crab densities for the section. At each of the three density categories I counted all 2 to 10 mm diameter burrows in two 0. 46 m^2 randomly placed quadrats. I then multiplied the width of the mudflat with weighted average burrow densities to calculate a crab abundance estimate for the sampling section. All crab prey sampling was conducted between 08:00 to 13:00 at 0.7 to 1.0 meters above lowest low water (based on published tide table values) on 15 to 25 July of 2004 and 2005. Although direct counts of *Scopimera* densities would have yielded more accurate estimates of prey availability than burrow counts, my method was necessitated due to the large number of sites that needed to be sampled over a short period (Yasué and Dearden, 2006c) . Moreover burrows were a good indicator of crab availability because crabs created burrows at every low tide period to feed at the surface (Takahashi et al., 2001).

Although my prey sampling was conducted late in the breeding season, the adults (and chicks if breeding attempts were successful) still remained in the territory when I was sampling. As pairs nested several times in the same territory, it is likely that pairs remained together defending the territory even after chicks fledged or a breeding attempt failed because of the possibility of renesting within the season.

3) Sex-roles during chick-rearing

I conducted 109 hours of brood watches at 57 different nesting attempts from a hide or a seated position at least 200 m away. Chick-rearing observations lasted 45 minutes to 1 hour (mean length = 50.2 ± 1.3 min).

I conducted scan samples and recorded the behaviour of the adults and chicks every five minutes as well as any types of anthropogenic or natural disturbances (Martin and Bateson, 1986).

Behaviour was categorized in the following manner:

Disturbed = Neck out-stretched vigilant posture, flushing to the mudflat from nest, "rat-running", calling to distract predators, false brooding or crouching (Gochfeld, 1984).

Territorial = Fluffed out feathers and displaying to, chasing or fighting with conspecifics.

Roosting = Body trunk on the ground, or eyes shut and feathers fluffed, preening feathers or bathing.
Feeding = Pursuing prey.
Nesting = Incubating eggs (occurs when chicks hatch asynchronously or successive clutches are laid before primary clutches fledge and one adult incubates clutches while the other cares for the chicks).
Brooding = Shading or brooding chicks.

I also estimated the distances between chicks to parents by counting body lengths or comparing to known distances. If there was more than one chick in the brood I estimated the distance from the adult to the nearest chick.

Malaysian plovers may have biparental care throughout the breeding season because both parents are required to defend chicks from predators and fledge chicks. In 71 brood observations people or potential predators disturbed broods at least once. I examined how chick age influenced the frequency of disturbance responses that were male-only, female-only or biparental.

4) Focal observations

In addition to nest or brood observations, I conducted 5 – 25 minute focal observations using hand-tallies and timers to measure adult activity budgets (Martin and Bateson, 1986). These focal observations were conducted between November and July and allowed us to detect any behavioural differences between males and females prior to, and during, the breeding season. During all observations I recorded the breeding status of the bird (pre-breeding, inactive, nesting, chick-rearing). *Pre-breeding* (pairs that had not yet laid clutches that year; generally Nov-March); *Inactive* (birds that had recently failed or fledged a chick, and not yet re-nested).

Finer behavioural categories were used during focal observations to detect rare or inconspicuous behaviours that may not be observed during brood observations. The roosting category used in brood observations was divided into resting, preening and bathing. I also included a category for courtship behaviour (nest building, copulating or displaying to mates). For feeding, I counted the number of attempted feeding attempts rather than the total amount of time birds appeared to be feeding. This approach was necessary to reduce ambiguity and facilitate comparisons between birds at different breeding stages because feeding birds were often also engaged in other activities such as defending territories or watching chick.

During focal observations, "disturbance" behaviour did not include neck-outstretched vigilance behaviour and only included times when birds were using calls and displays to distract predators, running or flying away from disturbances or crouching to hide from avian predators. This distinction was necessary because when adults were not rearing chicks it was often difficult to discern between vigilance from predators and standing and looking for prey or intruding conspecifics. When adults were with chicks it was easier to discriminate between vigilance behaviour and other non-disturbance related behaviour because adults were usually facing towards chicks and also frequently on the beach (rather than the mudflat feeding area). I also included one other category, "standing", to describe birds which were not overtly engaged in any of the other activities. In this position, birds may be passively looking for predators, prey or conspecifics or resting (but not sitting, preening or bathing). I did not conduct focal observations on plovers that were incubating nests.

I was able to ensure that an individual was not sampled more than once a day because birds were highly territorial and 65 % (2004) and 70 % (2005) of the birds were individually colour-banded.

Statistical analysis

All data analyses were two-tailed and conducted using SPSS version 11 (SPSS, 2001).

I used a paired t-test to evaluate whether there was any difference in the number of males and females in flocks at the five roosting areas prior to the breeding season.

Multiple incubation observations were taken from the same pair at the same nest, at different nests or between years. The total number of samples per individual ranged from 1 to 10 observations. I could not conclusively determine whether I resampled the same individuals between years because not all individuals were colour-banded. However, for incubation observations I randomly sampled one observation for each known pair in which I conducted multiple watches. Only one sample was taken for each pair between the two years. This approach was used instead of taking mean values of male and female attendance because temperature has a strong effect on incubation behaviour (Yasué and Dearden, 2006b) and mean values would obscure this effect. I used a Wilcoxon's Signed Rank Test of Related Samples to determine whether males and females had significantly different attendance during 82 nest observations.

I used binary logistic regression to test whether modelled egg temperature, prey availability (crab burrow relative density), embryo age (measured as weeks into the incubation period, 1 to 4), and time of day influenced total, male and female nest attendance. Time of day was included in the model to account for non-temperature-related factors such as predation or prey availability that could vary during the day. The incubation requirements of clutches may vary in a quadratic or linear function because birds must warm eggs at low temperatures and shade eggs at very high temperatures. Consequently I included both a linear and quadratic term for modelled egg temperature.

To conduct binary logistic regression, I categorised the three dependent variables into two equal-sized classes (Total attendance > or ≤ 80 %, male contribution (> or ≤ 17 %) and female contributions (> or ≤ 49 %). Binary logistic regression was used because data were not normally distributed and could not be normalized using standard data transformations due to the large numbers of zero values. To ensure the robustness of my models I reran the analysis five times on different subsets by randomly sampling different observations from the same pair. For all model coefficients and significance values I present mean value from the five analyses.

I also used a paired approach which allowed us to control for differences between individuals, or nest location, to assess whether the sexes responded differently to variation in modelled egg temperature. This method allows us to better detect interactive effects between sex and temperature. In the two years I conducted more than one incubation observation from 43 nests. I compared the nest attendance between the highest and lowest modelled egg temperatures observations from repeated observations of the same clutch. I only included one set of paired observation for each breeding pair of plovers. I conducted a Wilcoxon's Signed-Rank Test of Related Samples to examine differences in male and female nest attendance between the paired nest observations.

The above analysis can only assess how the rank (ie. lower [Lr] or higher [Hr] temperature) in paired observations affects male or female attendance. Absolute temperature (T_{La} and T_{Ha} for low and high absolute temperatures respectively) is likely to influence the difference in attendance between the two observations. I divided the 43 paired observations into two groups based on the modelled egg temperature from the higher observation of each pair (> or <= 36 C^0). There were 21 and 22 pairs in the low [La] and high [Ha] temperature category. The mean difference between the Lr and Hr of each pair was independent of the absolute temperature ($[T_{LrHa} - T_{HrHa}] - [T_{LrLa} - T_{HrLa}] = D_T = 0.98 \pm 0.57\ C^0$, $t_{41} = 1.6$, $P = 0.10$). I ran a Wilcoxon's Test of Related Samples for the two absolute temperature categories (Ha and La) separately. I also tested to see whether absolute temperature category influenced the difference in attendance between the sexes at the low and high temperature pairs ($[AM_{Lr} - AF_{Lr}] - [AM_{Hr} - AF_{Hr}]$ at Ha or La).

For each observation on chick-rearing plovers, I calculated the percent of scans in which males and females spent feeding, defending territories and responding to disturbances or watching for predators. I also calculated a mean chick to adult distance for each observation period. Any repeated observations from the same brood in a year were averaged and this mean value was used for the subsequent test. I ran a Wilcoxon's Signed Ranks Test of Related Samples to assess whether the frequencies of various behaviours and chick to adult distances differed between mates of the same pair. Between the two years, 11 pairs managed to double-brood, I did not conduct any repeated observations on the same pair at different nests. For this and subsequent analysis from observations on chick-rearing adults, I ensured that I did not resample the same individual between the two years by only including individuals that were colour-banded at the end of the 2004 breeding season and not sampled in 2005, along with all individual from 2005. It was reasonable to assume that no birds lost all four bands (three darvic and an aluminium band) between 2004 and 2005. For chick-rearing adult observations 44 different pairs were sampled between the two years.

To test the effect of chick age on the prevalence of behaviours and adult to chick distances, I only included the broods in which I had replicate samples for the same breeding attempt at different chick ages (120 observation periods of 33 broods). I created two categories based on chick ages (less than or greater than 15 days old). For each of the 33 broods, I calculated mean frequencies for territorial behaviour, vigilance and feeding and mean adult to chick distances for the two age categories. I compared the behaviour frequencies and distances between the two chick age categories for males and females using a Wilcoxon's Signed Ranks Test of Related Samples.

Using a chi-square analysis, I tested whether chick age influenced the frequency of biparental defence chick defence, male-only defence and female-only for the 71 disturbance watches (39 pairs) in which a potential predators or a neighbouring conspecific disturbed chicks. For this analysis I pooled data from broods 1 and 2 weeks old and also 3 and 4 weeks old to increase the number of observations in each category. If there were multiple disturbances in a brood watch, I used the most frequent type of response during the entire observation period for the analysis.

To examine the potential fitness benefits of defending territories, I used a binary logistic regression to determine whether the percent of scans in which male or female plovers spent defending territories from conspecifics influenced the likelihood of a nesting attempt fledging at least one chick. In total 54 and 83 chick-rearing adult observations were conducted at 22 and 34 different breeding attempts in 2004 and 2005, respectively. I used mean values of territoriality for replicate watches from the same breeding attempt and I did not sample the same brood at different nests in the same year. Between the two years I obtained both breeding success and behavioural observations from at least 44 different pairs of plovers. The potential reproductive benefits of territorial behaviour may depend partly on the density of other Malaysian plover nests. Thus I statistically controlled for breeding density (number of nests within 200 m of nest site using GPS coordinates) and year by including it into the logistic model (Hosmer and Lemeshow, 2000).

Differences in habitat quality could confound results on the effect of territorial behaviour on breeding success. A previous study on habitat-specific breeding success suggested that 0.5 to 5 m tall vegetation backing beaches provides cover for Malaysian plovers chicks and enhance fledging success (Yasué and Dearden, 2006c). Consequently, I also visually estimated percent cover of 0.5 to 5 m tall vegetation along three 50 cm wide transects running perpendicular to the tideline and extending 20 m into the vegetation from the beginning of the vegetation line on the upper shore of the beach (Daubenmire, 1959). This measure of percent vegetation cover was also included in the logistic model to predict fledge success.

For focal observations, behavioural data (time budgets) were standardized to percent time. In total 1291 focal observations were conducted on plovers at various breeding stages during the two years. However to reduce pseudoreplication I calculated mean values for each individual in each of the four breeding status categories for each year. For any individual in which I had multiple values for different breeding statuses or years I randomly selected one sample. I excluded observations from unbanded birds. I obtained 71 and 80 focal observations from banded male and female plovers and this included 33, 14, 18 and 15 observations from adult plovers that were known to be pre-breeding, inactive, nesting eggs or rearing-chicks. I did not record breeding status for all individuals in which I conducted focal observations. I used a Kruskal-Wallis test to assess whether there were any differences in the time spent defending territories, responding to disturbances or feeding rates due to breeding status for each sex. If breeding status affected behaviour, I tested to see if there was any difference between the sexes separately for different breeding status categories. I used a Mann-Whitney test of independent samples to determine whether sex affected the prevalence of any of these behaviours.

All error bars in figures denote standard errors.

Results

1) Sex ratios in wintering flocks

At all five locations there were, on average, a greater number of males than females in the pre-breeding flocks (Males 6.5 ± 0.84; Females 4.8 ± 1.0 individuals). However this effect was not statistically significant, likely due to the low sample size and statistical power (*Paired t-test* on log-transformed data $t_4 = 2.6$, $P = 0.063$).

These dense roosting flocks of six to fifty-one individuals were located within five 100 - 200 m wide beach sections. The larger flocks tended to occur at high tide in the early winter months (November to January). In February and March the flock sizes decreased as pairs dispersed and began to defend territories at nearby beaches. Sixty-eight percent of the 54 colour-banded birds that were captured in winter flocks at these three beach sections in 2003 later bred within 1 km away. Of these 54 birds eight did not breed within the study area in 2004, but returned to breed in 2005. The beach sections where birds roosted had the highest nesting densities and earliest clutches and thus appeared to be high quality breeding areas.

2) Nest attendance and incubation

Females incubated the eggs for a greater proportion of the observations than males (Males = 0.26 ± 0.028, Females = 0.41 ± 0.033 proportion of total nest observation, Wilcoxon's Signed Ranks Test of Related Samples $z = -3.2$, $P < 0.001$, $n = 80$ nest observations). On average, the nest was incubated for 0.67 of the observation period, and both sexes participated throughout the incubation period (Figure I-2).

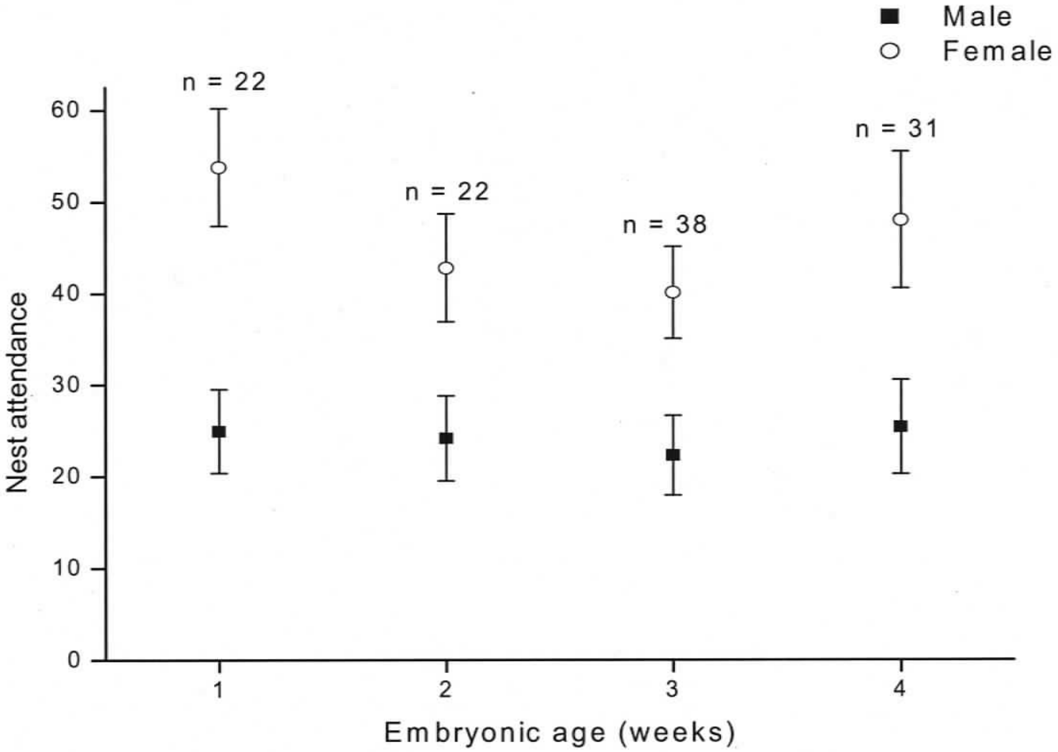

Figure I-2 Male and female incubation behaviour.
Variability in male and female nest attendance (percent of time nest incubated, 163 hours total) throughout the 4 week incubation period. Embryonic age had no effect on total attendance or on the relative contributions of the sexes.

Nests were more likely to be incubated during hot weather (Binary Logistic Regression final model coefficients: $\chi^2_1 = 8.8 \pm 1.2$, $P = 0.006 \pm 0.003$, $n = 82$, Factor coefficients: $b = 0.26 \pm 0.02$, Wald = 7.3 ± 0.9, $P = 0.010 \pm 0.004$, Receiver Operator Characteristic Area Under Curve ROC AUC = 0.72 ± 0.01)[**Figure I-3**] . For this and subsequent analyses, I did not include the quadratic term in the final model because it was not significant when I included both the linear and quadratic term in the models. Crab burrow relative density ($P = 0.88 \pm 0.02$) and embryonic age ($P = 0.80 \pm 0.01$) and time of day ($P = 0.50 \pm 0.02$) had no effect on total nest attendance and were removed from the original model.

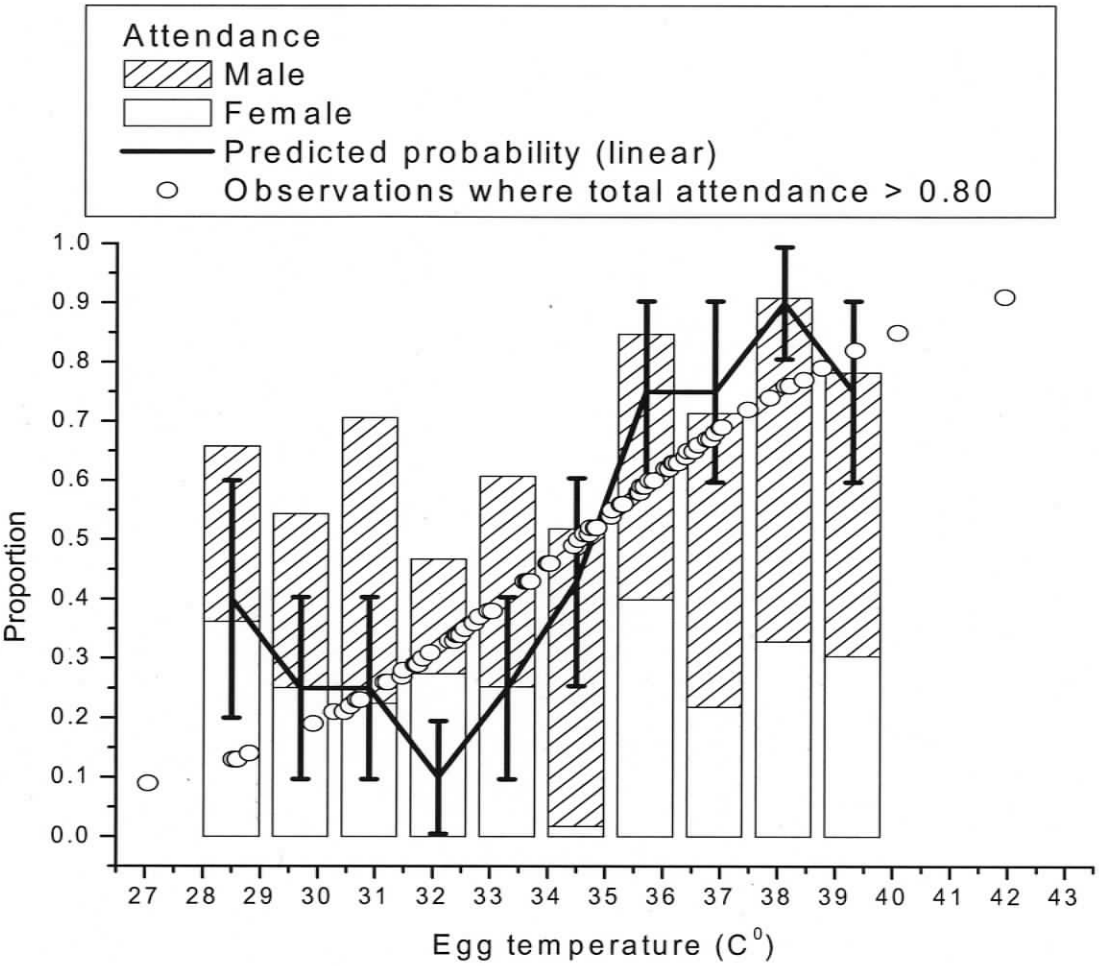

Figure I-3 Exposed egg temperature and attendance.
Total nest attendance was greater at higher modelled egg temperatures. The black line represents the proportion of incubation observations where total nest attendance was greater than 0.80 for each temperature category. Sample size for each temperature category ranged from 5 to 10 and total sample size was 82. Shown also are binomial error bars. The stacked bars show male and female attendance and the top of the stacks represent observed total nest attendance. White circles represent fitted logistic regression curve showing the predicted probabilities from the model. The bar graph and the logistic curve are plotted on the same scale.

Male nest attendance was not influenced by modelled egg temperature ($P = 0.32 \pm 0.05$). It appeared that egg temperature had a weak affect on female attendance ($\chi^2_1 = 3.5 \pm 0.19$, $P < 0.062 \pm 0.008$, $b = 0.17 \pm 0.009$, $Wald = 3.3 \pm 0.2$, $P = 0.061 \pm 0.011$, ROC AUC = 0.63 ± 0.001). Crab burrow relative density ($P = 0.95 \pm 0.01$) and embryonic age ($P = 0.952 \pm 0.001$) also had no effect on the male contribution to nest attendance. Female attendance was not affected by egg temperature ($P = 0.51 \pm 0.02$), crab burrow relative density ($P = 0.45 \pm 0.04$) or embryonic age ($P = 0.36 \pm 0.01$).

Based on the 43 paired observations of the same clutch at the highest and lowest modelled egg temperatures, female attendance (Nest attendance for Lr and Hr: 0.35 ± 0.05, 0.53 ± 0.04, $z = -1.15$, $P = 0.25$) and total attendance (0.66 ± 0.05, 0.84 ± 0.03, $z = -3.05$, $P = 0.002$) was affected by egg temperature but male attendance was not (0.31 ± 0.05, 0.31 ± 0.04, $z = -1.15$, $P = 0.250$) [

Figure I-4]. When I split the data into two categories based on the higher temperature value and reran the analysis it appeared that temperature only had an effect on male and total attendance when temperatures were greater than 36 C^0. Females adjusted attendance at both high and low temperatures. There were statistically significant differences in attendance between the sexes in the high and low temperature pairs when modelled egg temperature was less than 36 C^0 ($[AM_{Lr} - AF_{Lr}] - [AM_{Hr} - AF_{Hr}]$ when $T_{Ha} > 36$ C^0, $z = -0.016$, $P = 0.987$; $T_{Ha} <= 36$ C^0, $z = -2.31$, $P = 0.021$).

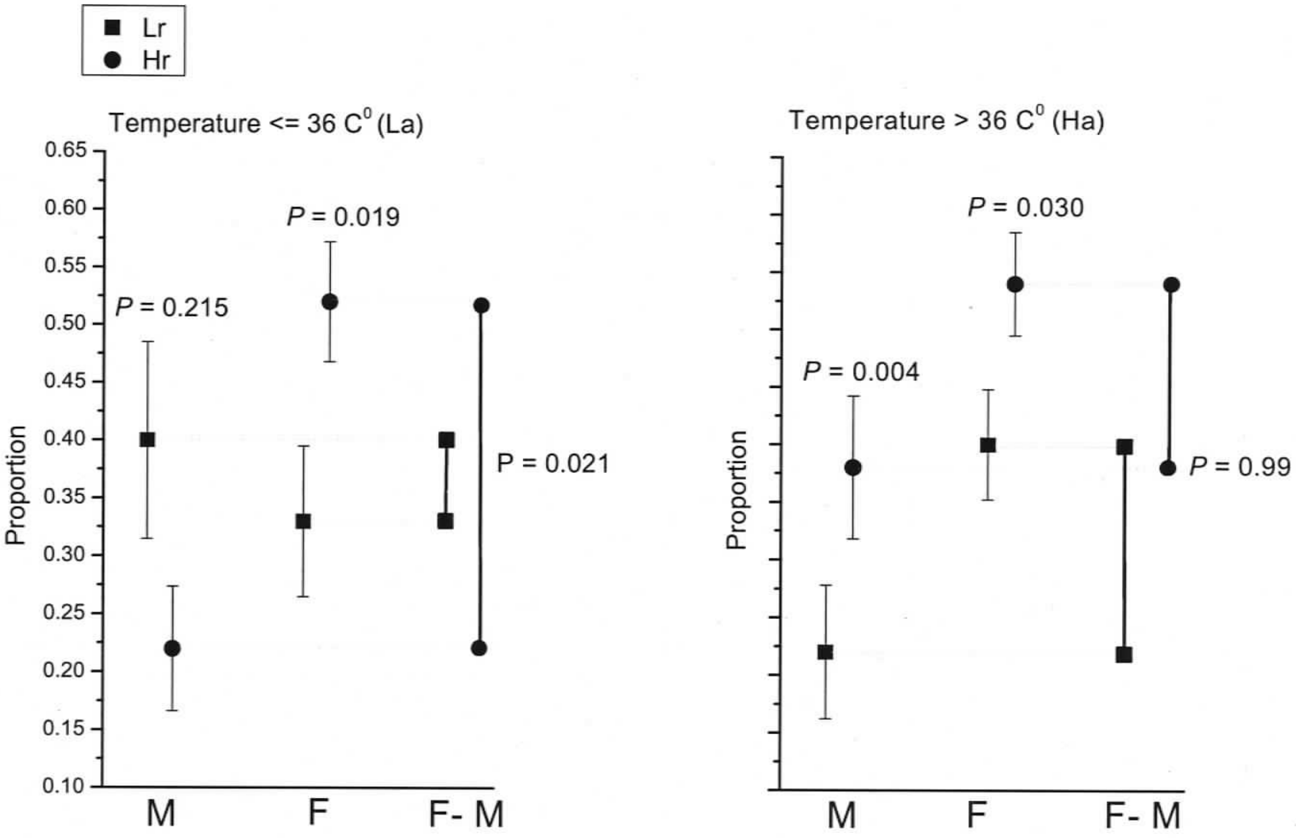

Figure I-4 Effect of sex and egg temperature on attendance

The effect of modelled egg temperature on male and female attendance at temperatures less (left) or greater (right) than 36 C0. Males only adjusted attendance according to temperatures during hot weather. The furthest two vertical lines (F-M in the X-axis) represent the mean difference between the sexes for each Lr and Hr pair.

3) Brood observations

In the 57 brood observations, males contributed more to territory defence (shown are male and female percent of scans throughout this paragraph: 3.7 ± 0.7 and 1.9 ± 0.5, z = -2.8, P = 0.002, n = 57 broods) while females spent more time roosting (3.9 ± 1.1 and 5.6 ± 1.7, z = -2.1, P = 0.04) and brooding chicks (3.5 ± 1.1 and 7.4 ± 1.9, z = -1.97, P = 0.049). There was no significant difference in the percent of time males and female spent feeding, grooming, incubating nests or exhibiting disturbance behaviour. Males and females spent 62 and 58 % of their time watching for predators or exhibiting disturbance behaviours and the contributions of both sexes to vigilance or chick defence appeared to be equal throughout the chick-rearing period (Figure I-5).

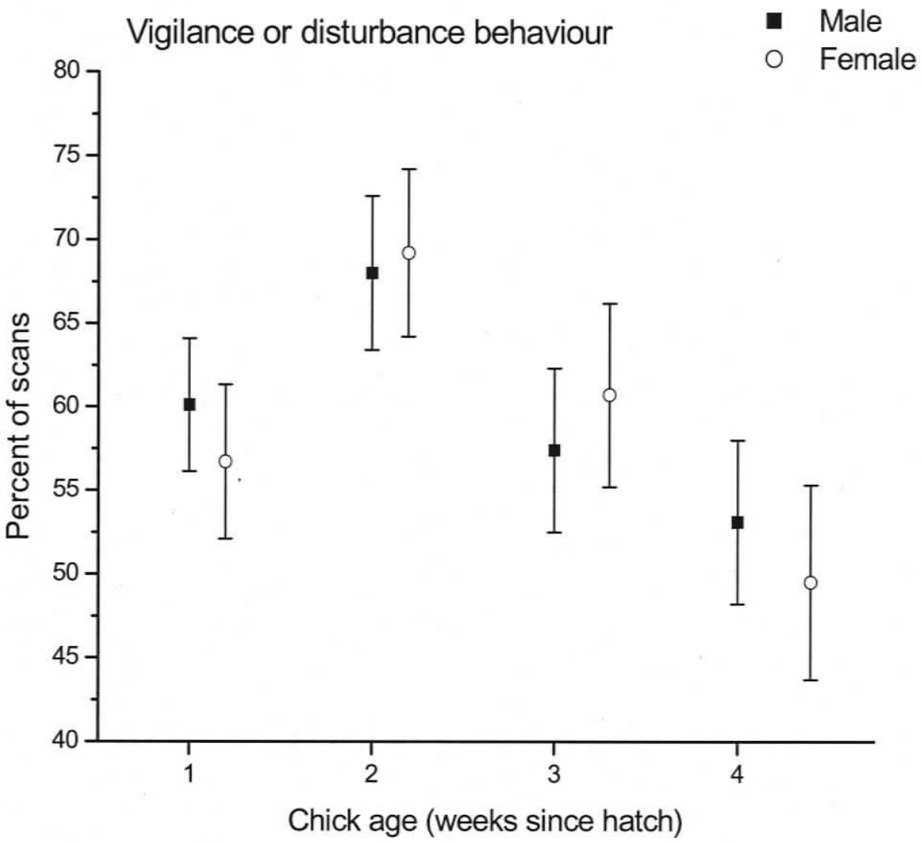

Figure I-5 Chick age and adult disturbance behaviour.
The amount of time chick-rearing males and females exhibited disturbance behaviour throughout the four week chick-rearing period.

In the 44 different pairs of plovers, males contributed a greater proportion of their time to territory defence and were significantly further away from chicks (Males 0.08 ± 0.005, Females 0.04 ± 0.008 z = -2.97, P = 0.004; and Males 15.0 ± 1.11 m, Females 13.3 ± 2.4 m z =-2.46, P = 0.014, respectively). There was no significant difference in the time males and females spent feeding or responding to disturbances or watching predator (Males 0.14 ± 0.02, Females

0.14 ± 0.02, z = -0.47 P = 0.64; and Males 0.61 ± 0.03, Females 0.59 ± 0.04, z =-0.41, P = 0.68, respectively).

For the 33 matched paired observations of the same brood at different chick ages, males were further from chicks when the chicks were older (z = -2.5, P = 0.012)[Figure I-6] .Chick age had no effect on female chick to adult distances (P = 0.35). Chick age and no statistically significant effect on the amount of time males or female spent feeding (Male and Females P = 0.17 and P = 0.61), defending territories (P = 0.13 and P = 0.15) or exhibiting disturbance behaviour (P = 0.13 and P = 0.98).

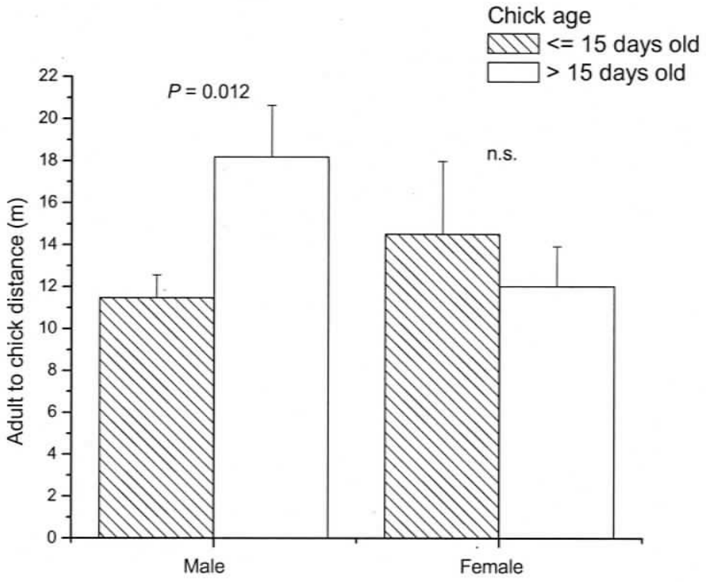

Figure I-6 The effect of sex and chick age on adult to chick distances

Both adults defended chicks during most human or predator disturbances. Chick age did not affect the frequency of biparental (64 % of 39 disturbances on different pairs), male-only (12.8 %) or female-only (17.9 %) disturbance responses (χ^2_3 = 1.59, P = 0.662, 24 and 15 samples were taken from chicks less than or greater than 15 days old, respectively). I could not assess whether the type of parental response influenced the success of nest defence from predators because there were very few diurnal predation attempts at my study site.

When I controlled for the number of conspecific nests within 200 m, percent cover of 0.5 – 5 m tall vegetation and year, both male and female territoriality contributed to greater fledging success (Binary logistic regression on 44 different pairs, Male Complete Model coefficients: χ^2_4 = 11.0, P = 0.027, Factor coefficients with only significant variable: Male b= 26.2, *Wald* = 7.8, P = 0.005, ROC AUC = 0.81; Female Complete Model coefficients: χ^2_4 = 10.3, P = 0.036, Factor coefficients with only significant variable b = 32.9, *Wald* = 7.0, P = 0.008, ROC AUC = 0.78 ; Figure I-7).

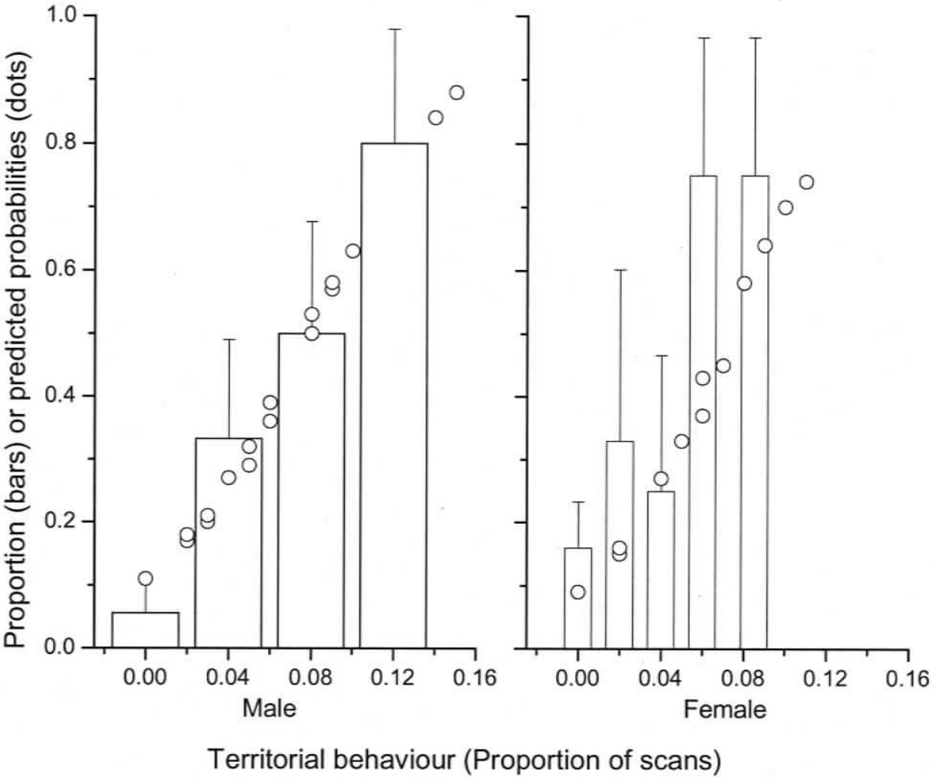

Figure I-7 Territorial behaviour and fledging success

Pairs that spent more time defending territories had a greater chance of fledging at least one chick when controlling for conspecific nest density and percentage cover of 0.5 to 5 m tall vegetation ($n = 40$ pairs). Bars represent the proportion of clutches that fledged at least 1 chick in each territorial behaviour category. For the highest category of territorial behaviour I pooled all higher values so that there was sufficient sample size ($n > 4$) in each bar. Binomial error bars are shown. White circles represent fitted logistic regression curve showing the predicted probabilities from the model. The bar graph and the logistic curve are plotted on the same scale.

4) Focal observations

Breeding status affected the number of feeding attempts for females (Kruskal Wallis test, $\chi^2_3 = 14.6$, $P = 0.002$, $n = 70$, pre-breeding season [1.73 ± 0.46], pairs without nests or chicks [1.72 ± 0.46], incubation [5.11 ± 1.43], or chick-rearing [0.84 ± 0.36]). Breeding status had no affect on the number of feeding attempts for males ($\chi^2_3 = 6.33$, $P = 0.096$). Breeding status had no effect on the total amount of time either of the sexes spent responding to disturbances (Male $\chi^2_3 = 5.3$, $P = 0.15$; Females $\chi^2_3 = 6.4$, $P = 0.09$) or defending territories (Male $\chi^2_3 = 0.91$, $P = 0.82$; Females $\chi^2_3 = 2.2$, $P = 0.54$).

Males spent twice as much time defending territories than females (Males: 2.2 ± 0.4 % time, $n = 80$; Females 0.83 ± 0.4 % time, $n = 70$; *Mann-Whitney test of independent samples* $z = -2.6$, $P = 0.013$). Territorial interactions occurred between males, males and females and only females. There were no significant differences in the number of feeding attempts between the sexes (Male 1.7 ± 0.29, Female 2.3 ± 0.39 attempts / min; pre-breeding season $P = 0.640$, pairs with no nests or chicks $P = 0.754$, incubation $P = 0.97$, or during chick-rearing $P = 0.060$), or disturbance behaviour (Male 1.34 ± 0.34, Female 0.95 ± 0.29 sec / min; $z = -0.72$, $P = 0.47$).

Discussion

This is the first detailed study on parental care in Malaysian plovers and one of the few studies examining how environmental factors affect breeding behaviour in a tropical shorebird. My study adds significantly to research on shorebird breeding ecology by quantifying behavioural differences between sexes from the non-breeding season in November to the chick fledging period in July and assessing how chick age and environmental factors influence the partitioning of parental duties.

The main differences between the sexes were that females contributed more to diurnal incubation, while males contributed more to territorial defence. Malaysian plovers shared parental duties throughout the entire breeding season and there was no indication that the egg-laying costs for females or lower parental certainty for males resulted in significant differences in overall parental effort. Both sexes built nests, incubated clutches, defended territories and protected chicks from predators, throughout the entire breeding period. This type of biparental care between the sexes occurs in some *Charadrius* plovers (Wallander et al., 2001), while other studies have demonstrated greater role division and desertion of clutches or chicks by one of the sexes (Walters, 1982; Warriner et al., 1986; Székely and Cuthill, 1999). In general, females adjusted incubation behaviour to changes in modelled egg temperature more than males. However, when temperatures rose above 36 C^0 males also increased incubation effort.

Females did not have higher feeding rates than males, and there was no detectable increase in male territoriality prior to egg-laying. This suggests that compared to some other shorebirds (Székely and Lessells, 1993; Oring et al., 1994), both female energetic constraints and risk of cuckoldry for males may be less important factors shaping Malaysian plover breeding strategies.

Female energetic constraints

Female Malaysian plovers may not have substantial difficulties acquiring and replenishing energy reserves to lay eggs because my study population had biparental incubation, relatively low incubation requirements for clutches and high and stable diurnal prey availability (Yasué, 2006b). Even females nesting in areas of low prey availability probably had sufficient time to meet energy requirements without reducing nest attendance because nests were rarely incubated during cloudy periods or after 16:00 in the afternoon. Total Malaysian plover nest attendance (67 %) was low compared to other related plovers which generally have diurnal nest attendance above 80 % and greater than 90 % for species with biparental incubation (Norton, 1972; Thibault and McNeil, 1995; Kosztolanyi and Székely, 2002; Wallander, 2003). Malaysian plovers probably had low nest attendance because incubation was not necessary for eggs to remain within optimal temperature range during most of the day. From late May to July in the Gulf of Thailand, it is cloudy in the afternoon and diurnal temperatures with cloud cover usually ranged between 33 and 37 °C.

The value of territorial behaviour

My study suggested that territory defence by both mates increased the chance of chick survival. Moreover males defended territories throughout the entire pre-breeding and breeding season and did not increase territorial defence efforts during periods when the risk of EPC was higher. These results suggest that male territorial defence should be considered *parental* (rather than *mating*) effort and that mates shared the fitness benefits of this behaviour. Territory defence probably improves breeding success because neighbouring plovers repeatedly chase and attack chicks in Malaysian plovers. Aggressive neighbours prevent chicks from feeding on mudflat and appeared to restrict chicks to less productive beach habitat that are closer to vegetation where chicks can hide when attacked by conspecifics (Yasué unpublished data). This type of aggressive conspecific behaviour has been observed in other plover species (Fraga and Amat, 1996; Teoh and Weston, 2002; Weston and Elgar, 2005a).

In addition to these immediate threats of conspecifics on chicks, for long-lived birds, with high site fidelity and multiple broods in a single season (Yasué and Dearden, 2006a), losing a territory during the breeding season may have significant costs to future reproductive success. Moreover maintaining the size of territories and preventing conspecifics from stealing territories is particularly important for my study population because recent coastal development projects have dramatically reduced the amount of suitable Malaysian plover breeding habitat (Yasué and Dearden, 2006c). Higher breeding densities that occur as a consequence of reduced habitat availability can cause prey depletion or enhanced nest predation and lower breeding success (Page et al., 1983; Sutherland and Anderson, 1993). Despite favourable energetic conditions for females to renest, relatively low required incubation effort and low nest or chick predation (Yasué, 2006b) neither the male or female abandoned clutches in order to renest with a different mate. Limited availability of high quality breeding habitat may be an important factor contributing to biparental care and mate retention (and thus habitats) throughout the breeding season.

Complementary sex-roles

Behavioural differences between the sexes could be largely due to an efficient allocation of parental duties based on differential abilities in the sexes for mutual gains. For example, plumage colour may be an important difference between the sexes because plovers nest on sandy white beaches and both their nest and chicks rely largely on crypsis to reduce predation risk (Kosztolanyi and Székely, 2002). During the day, female Malaysian plovers may contribute more to nest incubation and remain closer to chicks because predators are less likely to see females. Previous studies on related plovers (Fraga and Amat, 1996; Kosztolanyi et al., 2003) have also demonstrated higher females diurnal nest attendance.

It is also possible that females spend more time incubating nests or remaining close to chicks because males are better at defending chicks from conspecifics (Fraga and Amat, 1996). Although male and female plovers do not differ in body size, there could be other dissimilarities between the sexes such as testosterone levels, flight speeds or colour markings that could influence territory defence ability (Graul, 1973). In contrast to females that remain close to chicks near the beach, males often watched chicks and beach habitats from the mudflat. By having a wider vantage point, males may be more able to detect distant approaching predators and alert the more camouflaged females who can quickly lead chicks into the vegetation behind the beach and also defend both mudflat and beach segment of territories from conspecifics.

Alternatively females may incubate more during the day because males are better able to incubate at night (Jehl, 1973; Warnock and Oring, 1996; Kosztolanyi and Székely, 2002). Male-biased nocturnal incubation has been documented in many studies (see Wallander 2003 for review). These authors suggested that females incubate more during the day so that females can recoup body condition (Wallander, 2003) by feeding at night when there are fewer human disturbances (Burger and Gochfeld, 1991) or higher prey densities (Turpie and Hockey, 1993). This may not be an important reason for female-biased diurnal incubation because of the low incubation requirements of clutches (as discussed above) and low diurnal human disturbance rates at my study sites (Yasué and Dearden, 2006c). Moreover, their main prey, *Scopimera* crabs are more abundant in the early afternoon than at night (Yasue, M. Unpublished data, (Zwarts, 1990).

Previous studies also suggested that male nest attendance increased during periods of adverse weather (Norton, 1972). Both male Kentish plovers and common ringed plovers contributed to only a small percentage of diurnal incubation, and restricted these efforts to the hottest hours of the day (Wallander, 2003; Amat and Masero, 2004a). Malaysian plovers frequently cooled legs and bodies in pools of water prior to and immediately after incubation bouts. Male Malaysian plovers significantly improve both male and female fitness by incubating nests and preventing excessive heat stress that could impair female body condition and reduce hatch success (Ward, 1990; Amat and Masero, 2004a).

In contrast, temperature had no effect on female attendance. Female incubation may depend on other factors such as endogenous rhythms (Norton, 1972). A mate removal experiment in Kentish Plovers showed that males increased attendance after female removal, but females did not (Kosztolanyi et al., 2003).

Conclusion

For shorebirds that breed consecutively with the same mate within or between seasons, individual fitness is also affected by the condition of the mate (Wittenberger and Tilson, 1980). Thus birds may accommodate mates and adjust behaviour in response to varying environmental factors to successfully defend high quality territories, maximize the survival of the current brood and retain body condition of both sexes for future breeding attempts in the same or future years (Pierce and Lifjeld, 1998; Cuervo, 2003). The value of maintaining mutual body condition and the intensity of competition for space may also be particularly significant for other tropical, species because they are more often sedentary, may have higher mate fidelity, longer breeding seasons and higher survival rates (Sanz, 2001; Moreno, 2004).

Future research

Genetic fingerprinting to determine paternity would have improved the explanatory power of my study. Based on behavioural observations from my study, it appeared that EPC rates may be quite low in Malaysian plovers. They had biparental care, social monogamy throughout the entire breeding season, low copulations rates [0.18 copulations hour^{-1}, n = 501 focal samples, compared to previous studies (Birkhead and Møller, 1996; Pierce and Lifjeld, 1998; Wallander et al., 2001)] and Idid not observe any EPC's, or mate guarding. However, EPC's could occur at night (Double and Cockburn, 2000; Johnson et al., 2002).

Nocturnal studies on territoriality, foraging efficiencies and incubation duties are also important to compare parental effort and better understand the ecological factors contributing to different behaviours in the sexes (Kosztolanyi and Székely, 2002; Wallander, 2003). Although I detected changes in male incubation behaviour during the day, 24 hour studies are necessary to evaluate whether males increase parental effort, or if males increase diurnal parental care because females increase nocturnal incubation effort.

In this study I compared time budgets between sexes. However to compare the complete costs of parental care and reproduction between sexes it would be important to measure and compare the energetic cost of egg production along with field metabolic rate of several behaviours such as territory defence to measure cumulative energy expenditures (Nol, 1985; Brunton, 1988). Despite the potential for differences in prey availability and energetic considerations between tropical and Arctic species, very few energetic studies have been conducted in tropical environments. As I have demonstrated in this study, a better understanding of how environmental and ecological conditions affect the fitness maximizing decisions of tropical species may lead to a more complete analysis of the evolution of avian breeding systems and mating strategies.

II. Constraints on successive clutching behaviour for sedentary Malaysian plovers (*Charadrius peronii*) breeding in a tropical environment

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Abstract

In shorebirds, the prevalence of successive clutching and types of associated breeding strategies can differ between species, environments and individuals. Although several studies have examined successive nesting behaviour in holarctic species, little research has been conducted in the tropics. To assess the full range of reproductive strategies and better understand breeding constraints in tropical environments I characterized successive clutching behaviour in 54 and 79 colour-banded Malaysian plovers (*Charadrius peronii*) over two years in the Gulf of Thailand. As temporal variability in breeding conditions can affect the prevalence, timing of, and parental role-division between successive clutches, I also examined monthly changes in clutch size, clutch volume, prey availability and breeding success. Short renesting intervals, successive monogamy, high within-season site-fidelity, double-brooding and complete biparental care were general characteristic of successive nesting behaviour. I did not detect any changes in clutch size, clutch volume, prey availability and reproductive success during the course of the breeding season. For Malaysian plovers the stable and progressively favourable prey supply and weather conditions, lack of migration and intense competition for breeding habitats may have contributed to a breeding system constrained more by habitat availability rather than by time. In these environments pairs retain mates and cooperate to defend limited territories and chicks from conspecifics and breed multiple times during the long breeding season.

Introduction

Shorebirds are an excellent study taxa to examine the evolution of mating and parental care behaviour because they have immensely variable breeding strategies (Székely and Lessells, 1993; Parish et al., 1997; Amat et al., 1999a; Blomqvist et al., 2001). Part of this variability is a consequence of adaptations to different ecological and physical conditions (Székely and Cuthill, 2000). Although numerous studies have examined the breeding ecology of temperate and Arctic shorebirds, information on successive clutching on tropical species is largely limited to anecdotal observations in a small number of pairs (Jeffrey and Liversidge, 1951; Tyler, 1978; Thomas et al., 2003a). More research is needed to understand the full range of variability in shorebird breeding strategies and identify the environmental constraints that shape breeding behaviour in tropical species. In this study I examined the successive clutching behaviour of a sedentary shorebird, the Malaysian plover (*Charadrius peronii*) breeding in the Gulf of Thailand.

"Successive breeding" occurs when birds lay replacement clutches after failed attempts or try to fledge more than one brood in a single season (Blomqvist et al., 2001). The prevalence of renests, timing of successive clutches, parental role divisions and mate or site fidelity between clutches vary dramatically across and within shorebird species (Blomqvist et al., 2001; Andersson, 2005). The contrasting environmental conditions in holarctic and tropical areas may lead to differences in successive clutching behaviour between closely related holarctic and tropical shorebird (Johnsgard, 1981; Martin, 1996).

A key difference between holarctic and tropical environments is the degree of seasonal variability in prey abundance (Baker, 1938). High latitude environments are characterized by a brief burst of high prey availability followed by a progressive decline in productivity (Graul, 1976; Breiehagen, 1989; Smith et al., 1989; Sandercock et al., 1999). In these types of time-constrained environments, females may exhibit sequential polyandry or they may rapidly lay successive clutches ("multiple-clutching behaviour") during periods of high productivity (Oring and Knudson, 1972; Breiehagen, 1989). Females may have reduced body condition later in the breeding season and consequently they may be more likely to desert clutches, contribute less to parental care or produce smaller clutches or eggs (Rooneem and Robertson, 1997; Sandercock et al., 1999; Amat et al., 1999b). Females may also have greater difficulties attaining energy requirements to lay successive clutches and thus take more time to lay successive clutches (Nilsson and Svensson, 1996; Amat et al., 1999b; Amat et al., 2000; Blomqvist et al., 2001).

In contrast to holarctic shorebirds, tropical species may have longer breeding seasons because they generally migrate shorter distances and also have extended periods of favourable weather and a more stable prey base (Johnsgard, 1981; Martin, 1996). Longer breeding seasons could lead to greater replacement clutching (i.e. laying successive clutches after failed attempts) and double-brooding rates (i.e. laying successive clutches after successful attempts). Moreover, females may be able to have greater intervals between successive clutches and also show little seasonal declines in body condition (Pringle, 1987; Pierce, 1989; Dowding et al., 1999).

Shorebird parental care varies immensely within and between species. They may have partial or complete uniparental care by either of the sexes or sequential polyandry in which the male may care for the first clutch while the female incubates the second clutch (Graul, 1976; Erckmann, 1983; Breiehagen, 1989; Blomqvist et al., 2001), as well as complete shared biparental care (Lenington, 1980; Székely and Cuthill, 1999). The short breeding season in temperate or Arctic species may have lead to polygamous mating systems with partial or complete uniparental care (Graul, 1976; Bergstrom, 1988). Complete biparental care necessitates longer inter-clutch intervals because successive clutches are usually only laid after the fledge date of the primary clutch (Blomqvist et al., 2001).

In addition to the length of the breeding season, another key factor that influences successive clutching behaviour is the relative survival of young cared for by one versus two parents. In *Charadrius* plovers one mate may remain with the primary clutch while the other mate deserts the clutch close to, or after hatching to renest with a different mate (Székely et al., 1999; Amat et al., 1999a). This type of polygamous behaviour is adaptive for the deserting parent if the remaining parent is able to fledge chicks on its own (Székely and Williams, 1995) or if the survival probability of the current brood is low even if both parents contribute to parental care. Thus complete biparental care of successive clutches and longer inter-clutch intervals may be favoured in environments where nests and chicks are moderately vulnerable to thermal stress, predators or attacks from conspecifics and the cooperation of both adults increase fledge success rates (Erckmann, 1983; Dale et al., 1996; Reynolds and Székely, 1997). At present, there are not enough studies on tropical shorebird predation in order to assess latitudinal trends in predation risk for *Charadrius* plovers.Vulnerability to predators may vary more due to local conditions rather than between tropical and holarctic systems.

Other than descriptive census data (Collar et al., 1999; Robson, 2002) and recent concurrent research conducted in Prachuap Khiri Khan and Petchburi provinces, there have been no detailed studies on the ecology of the Malaysian plover (Yasué and Dearden, 2006a; Yasué and Dearden, 2006b; Yasué and Dearden, 2006c; Yasué et al., 2007). Malaysian plovers are an ideal study species to explore how environmental conditions could affect breeding behaviour because *Charadrius* plovers range throughout the world in high latitude, temperate and tropical environments (Johnsgard, 1981). Moreover extensive research has been conducted on parental care and breeding ecology of closely related temperate species (Bock, 1958) such as the killdeer (*C. vociferus*), Kentish or snowy plover (both *C. Alexandrinus*) or common ringed plover, *C. hiaticula* (Lenington, 1980; Székely and Lessells, 1993; Paton, 1995; Fraga and Amat, 1996; Wallander and Andersson, 2003). Moreover, along with 20 other tropical shorebirds, Malaysian plovers are threatened (IUCN, 2006) and a better understanding of the breeding and population ecology of tropical shorebirds could help provide the scientific base for effective conservation planning.

Here I conducted detailed behavioural observations and monitored breeding success in a population of banded Malaysian plovers to characterise the successive nesting behaviour and assess the extent to which energetic or temporal constraints and parental care requirements could have shaped this aspect of their breeding ecology.

Methods

1) Successive breeding behaviour

Study area

All data were collected within a 108 km stretch of sandy beaches in the Gulf of Thailand, between Bornok Beach (990 53′ 120 00′) in Prachuap Khiri Khan Province and Laem Phak Bia (1000 05′ 130 03′) in Petchburi Province between 15 November 2003 - 25 July 2004 or 10 January - 25 July 2005. In January and February, Malaysian plovers began defending 100 – 300 m long, multi-purpose territories that included an intertidal mudflat foraging area, a sandy beach for nesting and a shrubby vegetated area behind the beach that provided cover for chicks during disturbances. The weather from April to May tends to be hot, humid and sunny (diurnal temperature range 28 – 42 ^{0}C). Later in the season the weather becomes cooler, cloudier and wetter (26 – 38 ^{0}C).

Nest monitoring

I used noose mats or funnel traps to catch the majority of adults (65 and 70 % in 2004 and 2005) during the preceding winter or summer, on nests (Mehl et al., 2003). One-hundred and eighteen and 75 adults and 88 and 103 chicks were caught in 2004 and 2005. Using one of these methods, all but two birds that were targeted were caught. Of the 52 birds that were caught and banded in the winter of 2004, 38 did not breed within my study area. The 14 banded individuals that remained throughout the winter and breeding season, bred within 2 km, on the same beach they were banded. Fifty-three percent of the 66 breeding birds that were banded as breeders in 2004, returned to nest within 500 m of their 2004 nesting area in 2005. I captured and individually colour-banded chicks within two weeks of hatch and returned to the nesting territories every four to eight days for up to 30 days to assess chick survival.

In total, 86 and 126 nesting attempts of 54 and 79 pairs were monitored in 2004 and 2005. Data for the two years were analysed separately because there were substantial anthropogenic changes in habitat between the years (Yasué and Dearden, 2006c) and a larger area was sampled in 2005. Moreover, 33 of the pairs sampled in 2005 included individuals that were also studied in 2004 and so data were analysed separately to reduce pseudoreplication.

I surveyed beaches and mudflats for Malaysian plovers and found nests by searching in areas where pairs were observed or by watching birds return to nests. I visited the nests every three to five days to detect embryo mortality, estimate lay and hatch date by floating eggs (based on a 30 day incubation period and initiation of incubation after the laying of the first egg (Westerkov, 1950; Powell, 2001; Yasué and Dearden, 2006a). When nests or broods disappeared between checks, I recorded the nest failure date as the median date during the interval in which there were no nest checks (Mayfield, 1961). Close to the predicted hatch date, checks were conducted daily because of the high mortality rates of very young chicks. I was able to discriminate easily between failed and successful broods because chicks remained within 200 m of nest sites, chicks could be observed from a vantage point on the mudflat and adults with chicks conducted conspicuous displays while adults without chicks spent most of their time feeding and roosting in pairs on the mudflat and beach. If breeding attempts failed, I conducted extensive observations of the pair and recorded behaviours such as mate guarding, nest building or copulating so that I could determine whether pairs had renested.

Throughout the breeding season I surveyed additional beaches within 5 km of beaches with nesting Malaysian plovers once per month where plovers were not observed in the winter or during the early part of the breeding season, to ensure that I did not miss renesting attempts of banded birds that changed territories during the breeding season. Monthly surveys were sufficient to identify new nesting territories because plovers occupied territories for several weeks to months prior to nesting and remained in territories throughout the tidal cycle even prior to nesting or after failed breeding attempts.

In this study I defined renest interval for replacement nests as the days between primary nest failure and the lay date of the first egg in the successive clutch. I calculated mean renest intervals for pairs that renested more than once in a season. For pairs that attempted to fledge more than one clutch in a season (i.e. double-brooding, Blomqvist et al. 2001) I calculated renest interval as the number of days between the fledge date of the first clutch and the lay date of successive clutches ("inter-clutch interval" in this study). Although chicks that could fly occasionally remained with parents for up to ten days, I calculated inter-clutch intervals from when chicks were able to fly (27 to 33 days old). Flight ability was assessed by observing short distance practice flights of chicks and flushing chicks to force plovers to fly.

2) Parental care

I observed adults with nests and broods randomly throughout the day between 6:30 to 17:30 in 2004 and 2005. One to two hour incubation watches (mean length 75.7 + 2.3 min, *n* = 211) and 45 min to one hour brood observations (50 + 1.3 min, *n* = 134) were conducted between April and July on 113 and 57 different nests and broods. Between the years these observations were conducted on 95 and 54 pairs with nests or broods for a total of 163 and 109 hours. To minimise disturbances I observed the birds from a hide or a seated position on the mudflat more than 150 m from the plovers.

For incubation observations, I used a 15 – 45 X spotting scope and 10 X 50 binoculars to watch the birds continuously, record the sex of the bird on the nest, and record the start and end time of incubation bouts. During brood observations I conducted scan samples and recorded the behaviour of the chicks and adults at five minute intervals to assess whether both adults contributed to parental care.

In addition to these incubation or brood observations I also conducted 858, 5 – 25 minute long focal observations to detect any extra-pair copulations, new pairings or territory changes of Malaysian plovers. Adults were selected randomly and were only sampled once in a day. I was able to ensure that an individual was not sampled more than once a day because birds were highly territorial and most of the birds were individually colour-banded. The purpose of this part of the study was to assess mate or site fidelity and determine whether both sexes contributed to parental care. A more detailed evaluation of activity budgets and parental contributions during incubation and chick-rearing was examined in a concurrent study and will be presented elsewhere (Yasué and Dearden, 2007).

3) Seasonal variability

a) Clutch and egg size

I measured the maximum length and width of eggs using plastic callipers to the nearest 0.1 mm. I calculated egg volume (V) from maximum egg width (W) and length (L) using the formula (**Equation II-1**) used by Fraga and Amat (1996) on closely related and similar sized snowy plovers (Bock, 1958; Robson, 2002).

Equation II-1 Egg volume.

$$V = \left[0.5236 - \frac{0.5236 \times 2 \times L}{W \times 100} \right] \times L \times W^2 \qquad [1]$$

I used a Wilcoxon's Signed Ranks Test of Related Samples to determine whether individually colour-banded females laid smaller clutches with lower egg volumes than their earliest recorded nests in the season. If birds renested more than once in a season and I was able to record clutch volume for all renests, I compared the mean clutch size and volume of successive clutches to the earliest recorded nest.

b) Prey availability

Small *Scopimera* (bubbler) crabs are a major prey type for Malaysian plovers (Yasué and Dearden, 2006c). On three different beaches with nesting

Malaysian plovers, I sampled for *Scopimera* crab burrow density once per month at the same stage in the tidal cycle and between 11 am to 13:30 (according to published tide charts) from May to July in 2005. Burrows are a good indicator of crab availability because *Scopimera* crabs created burrows at every low tide period to feed at the surface (Takahashi et al., 2001). Samples were taken from the same 300 m length of beach for each of the three months to reduce the risk of confounding spatial and temporal variability. At each 300 m sampling section, I paced a transect perpendicular to the shore onto the mudflat and measured the width of the mudflat where crab burrows were present. Along each transect I sampled three crab burrow densities in 0.44 m^2 quadrats. Three to four transects were sampled at each beach for each sampling section. I multiplied the three crab burrow densities on a particular transect by the length of the mudflat that had crab burrows.

The data were converted to densities per m^2 and log-transformed (base-10) so that data approximated a normal distribution. I used an Analysis of Variance and a Tukey's post-hoc test to determine whether there was a monthly change in *Scopimera* crab burrow densities.

c) Breeding success

I also examined temporal variation in hatch and fledging probability based on daily survival estimates for clutches laid in the early (before May 15), mid (15 May – 15 June) and late (16 June - July) periods of the breeding season (Mayfield, 1961). I calculated the numbers of failed or successful nests based on the daily survival rates of nests and chicks and used this data in a Chi-Squared test of Independence (Dow, 1978). Time intervals were divided in this manner so that there was approximately the same number of nests in each date category. “Breeding success” is the probability that a clutch fledges at least one chick, “nest success” is the probability that clutches hatch at least one chick, and “fledge success” is the probability that a hatched clutch fledges at least one chick. In this study I could combine nest and chick success probabilities to calculate an overall “breeding success” probability because there was no significant difference in the length of the incubation and fledging period or survival for eggs or chicks in 2004 (Chi-Square test of independence: $\chi^2_1 = 2.00$, $P = 0.16$) and 2005 ($\chi^2_1 = 1.39$, $P = 0.24$) (Johnson, 1979).

Survival for 2004 and 2005 were analysed separately because there were significant differences in breeding success ($\chi^2_1 = 4.20$, $P = 0.040$) and habitat quality due to anthropogenic change between the years (Yasué and Dearden, 2006c). In addition, several pairs nested in both years and so pooling data together would have introduced pseudoreplication to the analysis. If there was more than one nest laid by the same pair during the same time interval in each year, I randomly selected one of the nests.

d) Likelihood of renesting

I tested whether date of primary clutch influenced the likelihood of renesting at least once using binary logistic regression. For this analysis I controlled for habitat characteristics that were shown to influence breeding success in a concurrent study. These variables were human disturbance levels (based on censuses of dogs and humans on the beach), predatory Ocypode crab densities on the beach, and the number of conspecific nests within 200 m for 2004 and the latter two variables were controlled for 2005. Human disturbance levels did not have significant effects on breeding success in 2005 (Yasué and Dearden, 2006c).

All data analysis was conducted using SPSS version 11.0 and all error estimates presented in text and figures are standard errors.

Results

1) Successive breeding behaviour

Prevalence of renesting

Almost half of the pairs (*n* = 54 and 79) that were monitored in 2004 and 2005 renested at least once in my study period. Of the banded birds that renested 67, 26, 5 % (2004) and 83, 14 and 3 % (2005) renested at least once, twice or three times. The majority of birds that renested did so after previous nests failed (**Table II-I**) .

Table II-I Renesting behaviour.
The number and percentage of Malaysian plover pairs that renested after failed and successful (> 1 chick fledged) breeding attempts in 2004 and 2005. Two right columns indicate the percentage of pairs that failed and then renested and the total percentage of pairs that renested (both renests and double-broods). Although all five of the pairs that double-brooded in 2004 were colour-banded, none of these pairs double-brooded again in 2005.

	Renest		No Renest		% Renest after failure	% Renest
Previous nest / Year	Succeed	Fail	Succeed	Fail		
2004	5	17	20	11	77	41
2005	6	30	14	24	83	48
	11	47	34	35		

I may have underestimated the proportion of renesting pairs because my study period did not extend to the end of the breeding season and nests have been documented until the end of July (Summer-Smith, 1981). However, I found substantially fewer nests in late June and July and the peak egg-laying period was between late April and May.

b) Renesting and inter-clutch intervals

The mean number of days between breeding failure date and lay date of the first egg of the successive clutch was 9.8 + 1.3 days ($n = 44$ pairs). In two cases, renests were laid when there was still one surviving chick.

On average, there were 4.6 days of overlap between successive clutches for pairs that attempted to double-brood (n = 11). The relative inter-clutch interval (days between laying of successive clutches divided by the total number of incubation and chick-rearing days) was 0.92 + 0.03 (Blomqvist et al., 2001). The greatest brood overlap was 12 days and the largest interval between the fledge date of the first brood and lay date of successive clutches was 8 days. It was not possible to conduct a statistical test on whether double-brooding actually increased breeding success because I was only able to measure fledging success in five (three out of five successive nests failed) and three (all three successive nests failed) of the eleven double-brooding pairs in 2004 and 2005.

In addition to successive double-brooding, one pair of plovers (both colour-banded) laid two clutches in a one week period 8 m apart and both adults contributed to the incubation of both clutches (Yasué and Dearden, 2006a). Although only one of these two clutches hatched, this is the first documented case of attempted simultaneous double-brooding in a shorebird.

c) Within season site and mate fidelity

Malaysian plovers had high site or mate fidelity within a breeding season in the study area. During brood, incubation and focal observations I observed no cases of extra-pair copulations and aside from territorial interactions with neighbours, adults were never observed outside of their own territories.

Of all renests for 78 colour-banded plovers only one individual renested in a different breeding territory. This male renested 5 km away from its primary clutch with a different mate and the former mate was never observed again during my study. Excluding this individual, renests were close to previous nests. In the eleven double-brooding individuals, pairs renested in the same territories with the same mate. Distance between successive nests after failed (60.3 + 15.2 m, n = 45) and successful (92.3 + 24.3 m, n = 10) breeding attempts were not significantly different from each other (Mann-Whitney's Test of Independent Samples z = -1.00, P = 0.32).

There were 62 renesting attempts by 52 colour-banded pairs and only five renests involved mate changes between successive nests. Of these five renests (three females and two males), one of the mates renested with a different partner within its original territory. It is possible that these mate changes were caused by the death of a former mate during the breeding season because I did not subsequently resight the former mate. For two of these renests, the individual that eventually switched mates initially remated with its former mate and renested with a new partner only after their nests failed a second time.

d) Between season site and mate fidelity

There also was high site and mate fidelity between the two years of my study. Fifty-three percent of the breeding birds that were banded in 2004, returned to nest within 500 m of their 2004 nesting area in 2005 (n = 80, **Table II-II**). The 38 banded birds that did not return to breed at 2004 nesting sites were not resighted within the entire study area in 2005. I visited additional beaches near my study sites and did not find any of the banded birds and so it is probable that some of these birds may have died between the two years. Half of the banded pairs from 2004 mated with their former mates in 2005. The remaining banded individuals either nested with unbanded mates or did not breed in the study area in 2005.

In contrast to the apparent high breeding site fidelity for adult plovers, of the 46 banded chicks that fledged in 2004 only three bred in the study area in 2005. For these three chicks, distances from natal site to 2005 breeding territories were between 3 and 13 km.

Table II-II Breeding site and mate fidelity.
Between season breeding site and mate fidelity of adult Malaysian plovers that were colour-banded at nests in 2004.

	n
Colour-banded breeding adults in 2004	80
Adults that returned to nest in study area in 2005 and nested:	
within 500 m of 2004 nest	42
Elsewhere in study area	0
Adult not present in 2005	38
Banded pairs of adults in 2004	32
Both mates returned to breed in 2005 and:	
retained mates from 2004	16
paired with different mates	0
One mate returned to breed and mated with an unbanded bird	10
Both members of pair did not return	6

2) Parental Care

Based on parental care and focal observations, all but two Malaysian plover pairs exhibited biparental care throughout the entire incubation period. In the two cases where one of the mates disappeared during incubation, the nest was abandoned in the next check and I never subsequently resighted the missing mate.

Throughout the entire chick-rearing period both parents remained within the territories and were present during all brood watches. Both parents brooded chicks and contributed to defending chicks from people, predators and attacks from neighbouring conspecifics. Although one parent sometimes fed on the mudflat more than 100 m away from older chicks, the parent usually returned quickly to defend chicks if there were any disturbances.

In the five brood watches that were conducted during the period when successive broods overlapped, both parents contributed to both chick-rearing of the primary clutch and incubation of the successive clutch. In addition, I conducted two disturbance observations on pairs which were concurrently rearing chicks and incubating successive nests. In these two cases the female remained on the successive clutch while the male conducted distraction displays. More behavioural observations are necessary to assess whether there are more subtle parental sex-roles during the brood overlap period between successive clutches.

3) Seasonal variation

a) Clutch size and egg volume

Four, 20, 75, 0.5 and 0.5 % of 205 nests had 1, 2, 3, 4 and 5 eggs respectively (mean clutch size 2004 = 2.8 + 0.067, $n = 46$ pairs; 2005 = 2.73 + 0.069, $n = 75$ pairs). Egg width, length and volume were 2.36 + 0.041 cm and 2.35 + 0.014; 2.92 + 0.04 cm and 3.14 + 0.016; and 8.25 + 0.24 cm^3 and 8.86 + 0.11 for 2004 ($n = 23$ pairs) and 2005 ($n = 70$ pairs) respectively. Clutch size and average egg volume did not differ between the first and mean successive clutches of the same female (Wilcoxon's Signed Rank Test of Related Samples Clutch size: 2004 $z = -1.29$, $P = 0.19$, $n = 19$; 2005 -0.38, $P = 0.71$, $n = 32$; Mean egg volume: 2004 $z = -0.51$, $P = 0.62$, $n = 7$; 2005 $z = -0.96$, $P = 0.36$ $n = 29$). For the five nests in 2004 and 2005 in which I measured the clutch and volume of more than one renest, there was also no significant difference between the first and last recorded clutch size (2004: $z = -1.89$, $P = 0.059$, 2005: $z = -1.00$, $P = 0.32$) and volume (2005: $z = -1.21$, $P = 0.23$). There were no nests in 2004 in which I measured volume in more than one renest.

b) Prey availability

There was no indication of a seasonal decline in prey availability (**Figure II-1**). Instead, prey availability appeared to be greater in June and July than in May (Tukey's test, mean difference May and June -0.31, $P = 0.002$, May and July = -0.47, $P < 0.0001$). Both month (Two-way Analysis of Variance $F_{2,96} = 14.51$, $P < 0.0001$) and site ($F_{2,96} = 10.44$, $P < 0.0001$) had significant effects on crab burrow density. The interaction term between the two factors was not significant ($P = 0.208$).

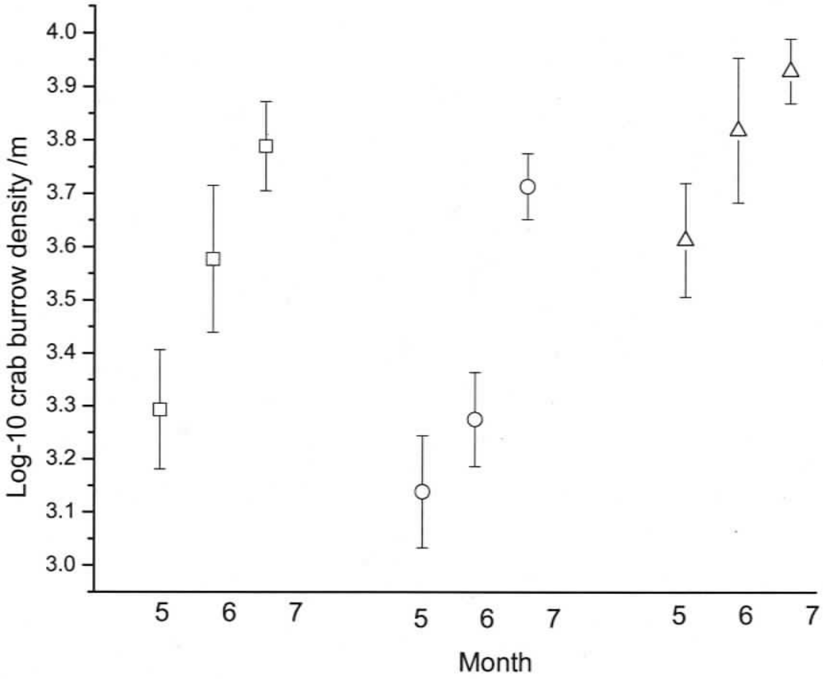


Figure II-1 Seasonal crab burrow densities.
Monthly abundance of *Scopimera* crab burrow densities at three, 300 m long mudflats sections adjacent to Malaysian plover nesting habitats in 2005. The three different symbols denote different locations. Between 9 and 12 densities samples were taken at each site and time interval.

c) Breeding success

There was no significant monthly change in overall Mayfield breeding success probabilities for 2004 ($\chi^2 = 0.67$, $P = 0.72$, $n = 57$ clutches) or 2005 ($\chi^2 = 2.72$, $P = 0.26$, $n = 82$ clutches). There were also no significant differences in hatch and fledgling probabilities when I analysed hatch and fledging probability separately (Hatch 2004 $\chi^2_2 = 2.64$, $P = 0.267$; 2005 $\chi^2_2 = 1.47$, $P = 0.480$; Fledge 2004 $\chi^2_2 = 1.30$, $P = 0.52$; 2005 $\chi^2_2 = 4.3$, $P = 0.12$, Figure II-2)

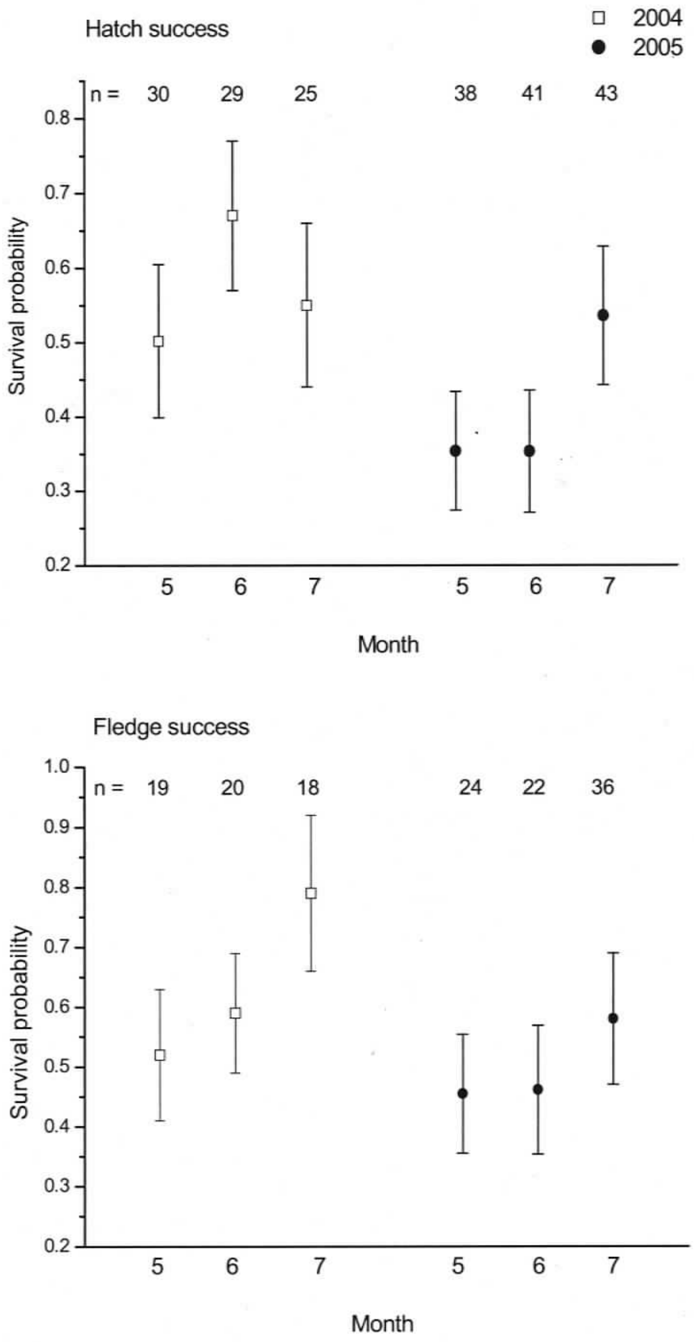


Figure II-2 Seasonal breeding success.
Seasonal variation in hatch (a, top) and fledging probabilities (b, bottom) in the Malaysian plover for 2004 and 2005. Success rates were based on daily survival estimates of clutches and chicks using Mayfield's exposure method (1961).

d) Probability of renesting

Pairs that laid their first clutch earlier in the breeding season were more likely to renest in 2004 (Binary logistic regression $B = -0.093 \pm 0.030$, *Wald* = 9.35, $P = 0.002$, Receiver Operator Characteristic Area Under Curve ROC AUC = 0.88, $n = 54$) and 2005 ($B = -0.035 \pm 0.031$, *Wald* = 7.04, $P = 0.008$, ROC AUC = 0.68, $n = 79$, **Figure II-3**) when I controlled for important habitat variables.

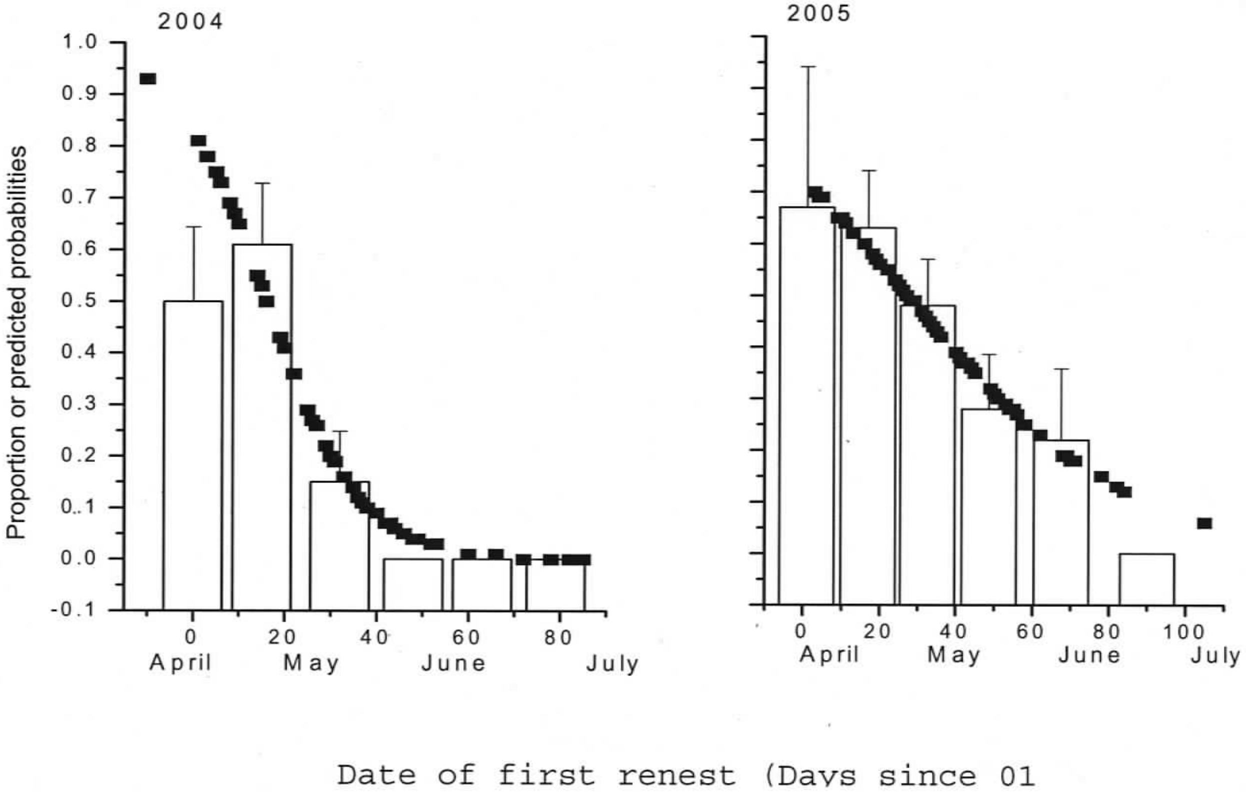


Figure II-3 Seasonal renesting probabilities.
Malaysian plovers pairs that nested later in the breeding season were less likely to renest in 2004 (left, $n = 54$) and 2005 (right, $n = 79$). The bars show the proportion of pairs that renested for each date category. Data were pooled for the latest date category so that there were more than three samples for each bar. Black dots represent a fitted logistic regression curve showing the predicted probabilities from the model.

Discussion

As far as I know, this is the first detailed study on successive breeding in a colour-banded tropical shorebird. The lack of seasonal declines in egg volume, clutch size, prey availability and breeding success suggests temporal or energetic constraints may be less important for Malaysian plovers compared to many migratory holarctic shorebirds (Lank et al., 1985; Sandercock et al., 1999). This may have this contributed to the short renesting intervals, successive monogamy, high within-season site-fidelity, double-brooding and complete biparental care in Malaysian plovers.

There are few detailed field studies on tropical species with which I can compare my results (Tyler, 1978; Cramp and Simmons, 1983). However sedentary populations in temperate southern hemisphere environments such as the New Zealand dotterel *C. obscurus*, red-capped plover *C. ruficapillus*, hooded plovers *Thinornis rubricollis* or white-fronted plovers *C. marginatus* also tend to have longer breeding seasons compared to holarctic species. High prevalence of successive clutching, short renest intervals and frequent double-brooding have been documented in these species (Summers and Hockey, 1980; Pringle, 1987; Pierce, 1989; Weston, 2000). Double-brooding occurs very infrequently in holarctic environments (as reviewed by Wallander and Andersson 2003)

Malaysian plovers renested many times in a season and renest intervals were shorter than documented in many previous plover studies (Warriner et al., 1986; Powell and Cuthbert, 1992; Fraga and Amat, 1996; Amat et al., 1999b).

For long-lived taxa such as shorebirds, costs to survivorship or future breeding potential limit the number of breeding attempts in a single year (Verhulst and Tinbergen, 1991; Nilsson and Svensson, 1996; Amat et al., 1999b). The energetic costs associated with egg-laying and parental care may be relatively low for Malaysian plovers due to the favourable environmental conditions (Morrison and Hobson, 2004). Females may be able to attain sufficient energy reserves to renest quickly because of the low thermoregulatory requirements and access to abundant and reliable food supplies (Hegyi and Sasvári, 1998). Throughout the entire study area there were wide mudflats with high *Scopimera* crabs densities immediately adjacent to Malaysian plover beach nesting habitat (*n* = 270 quadrats, 108 + 7.3 *Scopimera* burrows /m^2; Yasué, M unpublished data). There may also be lower survivorship costs to Malaysian plovers breeding late in the season compared to Arctic species (Nilsson and Svensson, 1996), because they do not undergo energetically costly migration shortly after breeding (Myers, 1981). Migratory populations of Kentish plovers tend to have shorter breeding seasons and single broods while mixed resident and migrant populations frequently have successive clutches (Boyd, 1972; Warriner et al., 1986).

Although both parents contributed to parental care throughout the entire fledging period, Malaysian plovers may still incur relatively low total parental care costs. On overcast days, temperatures in the study area usually ranged between 30 – 38 ^{0}C, which is close to the optimum shorebird incubation temperature of 36 – 38 ^{0}C (Webb, 1987). Consequently, nests were frequently left unattended for several hours in the late afternoons. This was particularly true in June and July as temperatures dropped and the rainy season began. During the day, nests were attended by one of the adults for only 67 % of the time (Yasué and Dearden, 2007), leaving ample time for adults to meet daily feeding requirements, gain energy reserves for future clutches or even care for a chick. Low nest attendance has also been documented in hooded plovers in warm climates in southern Australia (Weston, 2000). In holarctic environments birds may have to spend more total time incubating nests or brooding young chicks because of colder weather conditions (Norton, 1972; Martin, 1987; Visser and Ricklefs, 1993).

Parents may also expend relatively little energy searching for safe and profitable feeding areas for chicks. At the field sites Malaysian plover chicks fed on mudflats and beaches as well as wetlands or shrubby vegetation behind the beaches. Thus they could move and continue to feed in a different part of their territory if they were disturbed by people, conspecifics or predators. Moreover, the open structure of the beach allowed parents feeding on the mudflat to simultaneously watch chicks and defend territories from conspecifics.

The lower level of parental care required to fledge chicks may have also contributed to the occurrence of brood overlap in Malaysian plover. Although a few pairs of New Zealand dotterels, hooded plovers in Australia and ringed plovers in Germany have also demonstrated brood overlap, complete biparental care and no parental role division (Dowding et al., 1999; Weston, 2000; Blomqvist et al., 2001), my study is one of the first to demonstrate this behaviour in a significant number of pairs (11 different pairs between the years). Successive clutches were laid very close to the location of the primary nest. Thus adults could monitor a nest while watching a feeding chick on the mudflat. Parental role division may be more likely to occur in environments where adult feeding or chick-rearing areas are far from nesting habitats (Blomqvist et al., 2001).

Although both parents contributed to nest incubation and predator defence, the occurrence of brood overlap, low nest attendance rates and brooding effort (Yasué, M. unpublished), suggests that biparental care may not always be necessary for Malaysian plovers to successfully fledge chicks. This is most likely to be true later in the breeding season when clutches and chicks are less vulnerable to heat stress (Yasué and Dearden, 2006b). Biparental care may have also occurred as a consequence of limited high quality breeding territories (Haig, 1987; Haig and Oring, 1988). Intense competition for space may lead to difficulties securing breeding territories part way through the breeding season (Ens et al., 1992). By remaining paired throughout the breeding season Malaysian plovers have multiple opportunities to renest after nests fail or chicks fledge in high quality breeding territories. Plovers generally remained on the same territories for the entire breeding season. The paucity of alternate high quality habitats is also supported by the observation that plovers did not change territories even when there were dramatic reductions in habitat quality during the breeding season. During my two year study, resorts, roads and a seawall were constructed at 10 breeding territories (Yasué and Dearden, 2006c). When construction began during the breeding season, plovers did not change territories and instead suffered repeated nest failures due to trampling by heavy machinery.

High site or mate fidelity between successive nesting attempts have also been observed in some plover populations (Lessells, 1984a) but not in others (Warriner et al., 1986; Stenzel et al., 1994; Fraga and Amat, 1996). Previous studies have suggested that high mate and site fidelity occurs due to the greater time required to secure new mates or territories (Amat et al., 1999b). However as the breeding season is very long in Thailand, the low availability of high quality habitats in my study may be a more important factor contributing to both biparental care and social monogamy.

Approximately half of the population renested and half of the breeding attempts successfully fledged chicks. Thus for many pairs, successive breeding was an important strategy for plovers to fledge at least one clutch in the season. Successive breeding may be an adaptive strategy for long-lived species that live in environments with substantial intra and inter-year variability in breeding success (Page et al., 1983; Wallander and Andersson, 2003). During very good breeding years, birds can attain very high annual fecundity while incurring low costs to body condition in order to buffer years with low productivity (Strauss and Dane, 1989; Oring, 1993; Wallander and Andersson, 2003).

Successive breeding in shorebirds is thought to have evolved to bypass small clutch sizes and increase annual fecundity (Oring, 1993; Wallander and Andersson, 2003). In general, Malaysian plovers also had small clutch sizes. However there were three successful nests with unusually large clutch sizes. Although large clutches have been documented in Kentish plovers (Warriner et al., 1986), my observations are unusual because I did not detect additional females in the territory and it appeared that a single female laid all the eggs in a clutch. As Malaysian plovers were able to gain nutrients to quickly lay numerous eggs and successfully shade large clutches more research on tropical shorebirds breeding behaviour may provide greater insight on constraints limiting shorebird clutch size (Skutch, 1949; Arnold, 1999).

Despite the apparent lack of seasonal decline in breeding success, birds were less likely to renest if they bred later on in the season. One explanation for this result is that older individuals may be able to establish territories earlier in the breeding season, and may also be more likely to renest. Alternatively there could be other factors aside from prey availability, or weather patterns such as maximum tide heights or predation that could constrain the breeding season (Tulp, 1998). Unusually high tides increase flood risk for Malaysian and flooding was a significant cause of clutch failure at my study site (Yasué and Dearden, 2006c). Although maximum tide heights are high in January and February and could affect the start of the breeding season, tide heights were low throughout the summer and into the fall and consequently unlikely to have an influence on the end of the breeding season.

In a concurrent study I monitored causes of nest failure and documented any observations of diurnal predators. However, I observed very few attempts of diurnal predation (1 small Indian mongoose Herpestes javanicus and 10 Ocypode crabs), relatively low predation rates (38 and 32 % of failed nests in 2004 and 2005, compared to other *Charadrius* plover studies) and could not identify predators based on egg-shell evidence (Maybee, 1997; Yasué and Dearden, 2006c). More detailed predation studies using video recording at nests may help to evaluate how predation affects successive nesting behaviour.

Currently, almost all studies on avian breeding strategies have been conducted in north temperate environments, a region which includes less than one quarter of the global bird species (Moreno, 2004; Martin, 2004). Ecological and evolutionary research aimed at identifying the factors shaping parental care or mating strategies is hindered by the lack of data in tropical environments (Reynolds and Székely, 1997; Thomas et al., 2003a). In my research I suggest that many of the characteristics of a tropical breeding environment could have influenced the breeding strategy of the Malaysian plover. It is possible that biparental monogamous successive clutching and other unusual breeding strategies may simply be under-documented, due to the paucity of shorebird research in tropical environments. More research on tropical species may help to identify the social, ecological or physical parameters constraining breeding strategies and also determine the full extent of variability in shorebird breeding behaviour.

III. Simultaneous biparental incubation of two nests by a pair of Malaysian plover *Charadrius peronii*

Yasué, M. and Dearden, P. 2006. Wader Study Group Bulletin 109: 121-122

Abstract

There is tremendous variability in shorebird breeding strategies. Here I present the details of an unusual type of behaviour in which a pair of Malaysian Plovers *Charadrius peronii* laid two clutches within 8 metres of each other and the male and the female incubated both nests. Although shorebirds frequently nest more than once during a single breeding season, this is the first documented case where a double clutch was laid less than a week apart in the same territory with the same mate.

Introduction

Shorebirds may attempt to increase annual productivity by laying successive clutches in a single season (Reynolds, 1996; Blomqvist et al., 2001; Andersson, 2005). Numerous studies in temperate and Arctic environments have demonstrated substantial variability across shorebird species in the timing of successive clutches (Blomqvist et al., 2001), parental role division (Székely et al., 1999), and mate or site fidelity between clutches (Lessells, 1984b; Paton, 1995).

For some species such as the Temminck's stint (*Calidris temminckii*), spotted sandpiper (*Actitis macularia*) and mountain plover (*Charadrius montanus*) females will rapidly lay clutches with different mates and care for one ("multi-clutching") or none of the clutches ("successive polyandry") (Oring and Knudson, 1972; Graul, 1976; Erckmann, 1983; Breiehagen, 1989). In contrast to this type of polygamous behaviour, other shorebirds may retain mates, and lay successive clutches close to the fledge date of the primary brood ("monogamous double-brooding") (Blomqvist and Johansson, 1994; Dowding et al., 1999). For these species there may be either parental role division between the primary and secondary clutch or biparental care of both clutches (Blomqvist and Johansson, 1994; Parish et al., 1997).

In addition to variability between species, there may also be differences within species. For example, Kentish plovers (*Charadrius alexandrinus*) have both monogamous and polygamous breeding behaviour and the extent of parental care may vary between individuals (Székely *et al.* 1999). For polygamous individuals either the male or female may desert clutches during incubation or chick-rearing to renest with a different mate (Warriner et al., 1986; Székely et al., 1999; Amat et al., 1999a).

No published studies have examined the breeding ecology of the Malaysian plover (*Charadrius peronii*) throughout their range in Southeast Asia. During a study in the Gulf of Thailand, in which I monitored 86 and 126 nesting attempts of 54 and 79 pairs in 2004 and 2005, I showed that Malaysian plovers frequently laid successive clutches after failed or successful breeding attempts. They have short renesting intervals (9.6 days between nest failure and clutch initiation of successive nest), complete biparental care, high mate and site fidelity between clutches (1 out of 78 individuals changed territories and mates between clutches) and occasionally attempt to fledge more than one clutch in a season (9 % of pairs, unpublished data, M. Yasue).

Methods and Results

The simultaneous double-brooding pair nested on a 50 by 30 m sandy embankment adjacent to a 3 m wide river channel in Prachuap Khiri Khan Province (12o 03'N, 99o 54'E). I first discovered a male incubating the "primary clutch", nest A on 23 April 2004. After observing nest A I noticed a female incubating a different nest ("secondary clutch", nest B) only 8 m from the first nest. This was unusual because Malaysian plovers are intensely territorial and nests are on average 671 ± 166 m (mean ± SE, here and throughout text) from the nearest neighbouring nest. On that day, I floated the eggs and determined that Nest A had 3 eggs that were laid between 15 -18

April and nest B had two eggs that were laid between 17 - 20 April. The lay dates were estimated based on a 30 day incubation period and a floatation chart that was developed during the course of the study ($F_{1,42} = 62.5$, $P < 0.0001$, Adjusted $r^2 = 0.589$, **Equation III-1**). There were 21 nests in which I could confidently determine incubation period because I visited the nesting territory on the day before clutch initiation and on the day of hatch.

Equation III-1 Prediction of days to hatch.

$$Days = (12.05 \pm 0.58) - (0.48 \pm 0.061) \times D$$

Where D = Diameter of the area of the egg (in mm) that floats above the surface when the egg is placed in fresh water (Appendix 2).

On 06 May I returned to the nests to catch and colour band the pair using funnel traps. When I arrived at the site, a male was incubating nest B, and a female was incubating nest A. I was able to catch the male on nest B on the first try. However, when I set the funnel trap on nest A to catch the female, she walked around the funnel trap once, and then walked to nest B (where the male was incubating the nest), and then replaced the male and began incubating nest B. The banded male subsequently began to incubate nest A within the funnel trap. I waited for 30 minutes but the male remained on nest A in the funnel trap and the female continued to incubate nest B. Consequently, I switched the location of the trap again to try to catch the female, and again the female displaced the male and incubated the nest without the funnel trap. She continued to incubate this nest until I stopped my observations 15 minutes later. Based on these observations, I was certain that both mates were incubating both nests.

Over the next week I used a 15 – 45 X spotting scope and observed the nests from a seated position in the vegetation 80 m away from the nests to determine the proportion of time each parent contributed to incubating both nests. I continuously watched the nest and recorded the sex of the bird on each nest, and the start and end time of incubation bouts. Initially both mates incubated both nests and mates sometimes swapped nests after feeding bouts or if one of the mates did not return to a particular nest for over 15 minutes. At the end of the 07 May observation, I finally succeeded in catching and colour-banding the female. On all observations I checked the identity of the male and female plovers and scanned within 300 m of the nest for the presence of other unbanded plovers. No unbanded plovers were observed during the observations. From 15 May, nest A appeared to be abandoned, as the eggs were cold and there were no fresh plover tracks leading to the nest. After nest A was abandoned, I only observed the female incubating the remaining nest, but the male was always feeding, defending territory or roosting within 200 m of the nest. Nest B hatched two chicks on 21 May and both adults cared for the chicks. One chick died between 22 and 26 May and the other died between 29 May and 01 June. A successive two-egg clutch was laid between 30 May and 2 June within 30 m of the first two nests (**Table III-I**).

Table III-I . Incubation roles for simultaneous double clutch
Percentage of time nests were incubated by male (M) or female (F) Malaysian plovers during incubation observations between 07 May and 19 May 2004 for a simultaneously double-brooding pair. On 07 May only the male was individually colour-banded. Both sexes were colour-banded for all subsequent observations. Nest = N.

Date in May	Start time	Nest watch Duration (min)	Percentage of observation period							
			N: A	N: B	Male Attendance			Female Attendance		
			M + F	M + F	N: A	N: B	Total	N: A	N: B	Total
07	11:10	45	55	42	11	42	53	44	0	44
10	7:46	63	30	49	26	23	49	4	26	30
11	15:36	44	72	100	0	100	100	72	0	72
13	16:44	36	19	0	0	0	0	19	0	19
15	17:00	60	0	53	0	0	0	0	53	53
17	12:35	50	0	1	0	0	0	0	1	1
19	9:59	10	0	100	0	0	0	0	100	100

Discussion

In contrast to other double-brooding pairs in my population, the focal pair laid a successive nest before chicks from the "primary" clutch had hatched. This type of simultaneous monogamous double-brooding has been documented in other avian taxa (Burley, 1980). Amongst shorebirds, the most similar monogamous successive clutching behaviour has been observed in lapwing *Vanellus vanellus* in Sweden. However, these lapwing laid the secondary clutch near hatching of the primary clutch and there was parental role division between the clutches (Blomqvist and Johansson, 1994).

It is unclear why the one focal pair simultaneously double-brooded in 2004. In 2005 the pair returned to the same breeding location, but they did not simultaneously double-brood. The prey density in front of this habitat (120 ± 7.2 *Scopimera* crabs / m^2) was similar to the average density of all the sites. It is possible that other subtle differences in parental qualities or vulnerability to predators between this site and other areas or between the two years may have lead to the simultaneous double-brooding by this pair in 2004. I believe that the territory quality was relatively high because it was occupied early in the winter in both years and this pair was the fourth and fifth earliest to breed in 2004 and 2005. In addition, despite the fact that there were 500 and 800 meters of unoccupied territory to the south and north of the focal pair, in 2004 there was a conspecific nest of a banded pair unusually close to the focal pair (78 m away). There was intense fighting and repeated attacks on respective chicks and in 2005 the other banded pair did not return to the breeding site.

Currently, almost all studies on shorebird breeding strategies have been conducted in Arctic or north temperate environments (Thomas et al., 2003a). More research on sedentary tropical shorebirds may help to understand the unusual behaviour of this focal pair and identify the full range of ecological and environmental factors shaping mating strategies of parental care in shorebirds.

PART 2: POTENTIAL IMPACTS OF HABITAT CHANGE

IV. The potential impacts of tourism development on the habitat availability and productivity of the Malaysian plovers (*Charadrius peronii*)

Yasué, M. and Dearden, P. 2006. Journal of Applied Ecology 43: 978-989

Abstract

Tropical shorebirds are threatened by tourism development on beach breeding habitats. Few studies have examined the potential impacts of human disturbance and habitat change on tropical shorebirds. In 2004 and 2005, I monitored 54 and 79 pairs of Malaysian plovers in the Gulf of Thailand, and used logistic habitat models to identify factors influencing habitat selection and breeding success. These models included variables affected by anthropogenic changes such as human disturbance and vegetation structure, as well as other natural factors such as prey availability and predator densities. I also assessed causes of nest failure and conducted 372 hours of behavioural observations to identify mechanisms that relate the important habitat variables to plover productivity. Plovers selected wide beaches with low human disturbance that had a low percentage cover of tall trees backing the beach. The likelihood of hatching clutches and fledging chicks were greater in territories with low human disturbance, low conspecific density and high percentage cover of 0.5 to 5 m tall vegetation backing the beach. Nest monitoring and behavioural observations suggested that heightened vulnerability to tidal inundation, trampling, heat stress, predators and territorial conflicts may have contributed to the results from the habitat models. I concluded that tourism development on Thai beaches affect both habitat availability and productivity of Malaysian plovers by enhancing beach erosion rates, converting medium vegetation into tall monocultures and intensifying human disturbance. These direct effects of habitat loss may be exacerbated by density-dependent reductions in productivity. This study

demonstrates the value of combining three approaches: habitat modelling, nest monitoring and behavioural observations to identify impacts of anthropogenic changes and assign ultimate causes. In under-studied regions where there are pressing threats to wildlife, this type of approach may help to rapidly obtain the necessary data to assess and predict human impacts.

Introduction

Sandy tropical beaches have tremendous economic value (Clark, 1997) and are coveted areas for tourism development. Such development can lead to increased levels of disturbance and alterations in habitat structures that may threaten beach-nesting waders (International Wader Study Group, 2003; Weston and Elgar, 2005a). Although the effects of tourism development on temperate beaches has been widely studied (Lord et al., 2001; Ruhlen et al., 2003) there have been few studies in the tropics yet nearly 40% of red-listed waders breed in these areas (Baillie et al., 2004). Factors such as weather and predation that may influence the vulnerability of waders to tourism development (Flemming et al., 1988; Clark and Nudds, 1991) are likely to differ between temperate and tropical environments (Martin, 1996).

In this study I focused on the Malaysian plover *Charadrius peronii* Schlegel, a sedentary plover that breeds on quiet, sandy beaches in Southeast Asia. Malaysian plovers are red-listed, along with 11 other waders breeding in this region (Baillie et al., 2004). With some of the world's fastest growing economies and high human coastal densities, these waders are increasingly threatened by anthropogenic habitat change (World Resources Institute, 2004). However, no detailed or quantitative studies have been conducted on the breeding ecology or the potential impacts of development on the Malaysian plover or any of these other species.

The conflicts between tourism development and conservation are clearly evident in Thailand (Parr et al., 1993; Kontogeorgopoulos, 1999). With a 3000 km coastline and strong government support for tourism, beaches are rapidly being converted into resorts, restaurants and seawalls to meet the demands of international tourism as well as expanding domestic tourism (Kontogeorgopoulos, 1999).

Previous studies on temperate beaches have shown that human disturbance can lead to trampling of nests or chicks (Ruhlen et al., 2003), thermal stress (Weston and Elgar, 2005a), greater predation risk of chicks or clutches (Bolduc and Guillemette, 2003) and reduced feeding times for chicks that may lead to starvation (Leseberg et al., 2000).

Changes in habitat structure due to tourism development may also reduce habitat availability or breeding success. For example, changes in vegetation structure can influence both predator density and the vulnerability of waders to predators (Pampush and Anthony, 1993; Manzer and Hannon, 2005). In Thailand, one consequence of tourism-related development is the conversion of shrubby dune vegetation, mangroves or *Acacia* bushes to tall *Casuarina* trees (Bamroongrugsa, N. Wetlands International, unpublished data). These trees provide a shady environment with sparse underlying vegetation that is favoured by tourists. However, tall trees may provide perch sites and hence increase predation risk from avian predators (Wolff et al., 1999; Dekker and Ydenberg, 2004). Moreover the removal of ground-cover and bushes along beaches may reduce fledgling success because these types of vegetation provide cover for chicks from visual predators (Clark and Nudds, 1991; Pampush and Anthony, 1993). Furthermore, a reduction in beach width as a result of development may contribute to increased vulnerability of nests to flooding (Koenen et al., 1996a) and predation (Liley, 1999). Finally, in my study area there is substantial erosion partly due to the construction of seawalls and jetties at adjacent beaches (Brown and McLachlan, 2002).

In this study, I assessed how human disturbance and alterations in habitat structures influence habitat availability and fledgling success of Malaysian plovers, using logistic habitat models. These models included variables affected by anthropogenic changes such as vegetation structure, beach width and human disturbance, as well as natural factors such as prey availability and predator densities. Although previous studies have demonstrated changes in breeding distributions or productivity due to tourism development (Beale and Monaghan, 2004b; Finney et al., 2005), most studies have examined anthropogenic changes in isolation from ecological factors and have not identified the mechanisms leading to changes in productivity. It is important to measure a series of ecological variables because they reflect natural constraints on productivity and may influence the fitness impacts of development. Understanding the mechanisms by which anthropogenic changes affect productivity may help to quantify the impacts on wildlife (Gill and Sutherland, 2000) and identify the best management practices to mitigate these effects (Beale and Monaghan, 2004b). In order to interpret the results of my habitat model more effectively, I also conducted detailed behavioural observations and ascertained causes of nest failure to identify potential predators and other sources of disturbance.

Methods

Study area

All data was collected in four study areas in Prachuap Khiri Khan and Petchburi provinces in the Gulf of Thailand from 25 April to 25 July in 2004 and 2005. From south to north these study areas were: Bornok (BO, 99^{0} 53′ 12^{0} 00′), Khao Sam Roi Yod (KSRY, 99^{0} 56′ 12^{0} 05′), Pranburi River mouth (PR, 100^{0} 00′ 12^{0} 25′) and Laem Phak Bia (LPB,100^{0} 05′ 13^{0} 03′). PR was only monitored in 2005. Land uses ranged from pastures for cattle, coconut plantations and prawn aquaculture to roads, resorts and restaurants in more developed areas.

Between 2004 and 2005 there were substantial changes in land use. In 2005, four resorts were constructed along an 8 km beach in BO. Six resorts, a dirt road and a paved road were built on a previously undeveloped 5 km beach at PR in 2005. The most significant habitat change was at LPB. In 2004 there was little human disturbance at the north end of LPB because a 1 km long mangrove forest and river separated the 3 km long sandspit from any human structures. However in 2005 the mangrove forest and sandy peninsula were converted into a seawall during the breeding season. With many construction workers and a new dirt road allowing easier access to the area for local fishers, disturbance levels increased dramatically in 2005.

1) Monitoring of breeding pairs

The majority of plovers were caught and individually colour-banded either during the preceding winter, summer or on nests using noose mats or funnel traps (Number of banded adults : chicks 2004 and 2005: 118 : 88, 75 : 103). Sixty-five and 70 % of the breeding adults were banded. There were 48 birds that were caught during the winter of 2004 that did not breed in the study site.

I found nests by searching in areas where pairs were frequently observed or by watching birds return to nests. Eggs were floated regularly to detect embryo mortality, estimate lay date and hatch date (Westerkov, 1950; Powell, 2001). Eggs were laid over a two to four day period and incubation began after the first egg was laid. I assumed a 30 day incubation period based on 21 nests for which I was able to accurately measure incubation length (30.4 ± 0.95 days). I checked the nests every three to five days to determine nest survival or cause of failure. If any clutches less than 25 days old disappeared between checks and there was no sign of inundation (destroyed nest structure, tidal debris at nest) or trampling (crushed nest structure and eggs, tracks of vehicles and footprints) I assumed that nests were predated. This was a reasonable assumption because local people did not collect eggs for consumption. During nest checks I resighted adults to ensure that they were still present and thus discriminate between desertion and predation as cause of failure.

Close to the hatch date I visited nests every day and recorded the number of peeping or pipped eggs so that I could predict and visit the nest on hatch day.

This allowed us to discriminate between nests that were predated before hatch and successful nests in which the chicks died soon after hatch. Detailed observations of adults and chicks helped us determine whether nests had failed or succeeded. Adults with failed nests roosted or fed in pairs on the mudflat, whereas adults with young chicks conducted conspicuous distractive displays when I approached the nest site. I captured and banded chicks within two weeks of hatch and returned to the nesting territories weekly to assess chick survival up to 30 days. Family groups could be identified because at least one of the chicks or adults was colour-banded. Assessing fledgling success was not difficult because plovers were restricted to beach habitats and did not move more than 200 m from the nest sites. In total, 86 and 126 nesting attempts of 54 and 79 pairs were monitored in 2004 and 2005.

2) Habitat Model

Measurement of habitat characteristics

Malaysian plovers defended rectangular 100 - 300 m long, 5 – 40 m wide beach section and adjacent mudflats (20 – 400 m exposed at low tide). I characterized 200 m long breeding territories and random sites that included the mudflat, beach and vegetation backing the beach.

At each 200 m beach section, I measured the beach width at three transects 60 m apart. Percentage cover of ground-cover (height < 0.5 m), medium vegetation (height 0.50 m to 5 m) and tall vegetation (height > 5 m) were visually estimated along three 50 cm wide transects running perpendicular to the tideline and extending 20 m into the vegetation from the beginning of the vegetation line on the upper shore of the beach (Daubenmire, 1959). In 2005 I also used the same method to estimate the percentage ground-cover on the beach because vegetation may reduce an incubating plover's predator detection abilities (Wiebe and Martin, 1998; Amat and Masero, 2004b).

In 2005, there were strong correlations between the different height categories of vegetation cover backing the beach (*Pearson's* r 0.13 to 0.65). Thus I used factor analysis and reduced the three variables (short, medium and tall vegetation) into two orthogonal variables that accounted for 70.0 % of the variance. Component 1 described territories with dense medium vegetation cover (Correlations with independent variable and principal components r = 0.88) and low percentage ground-cover (r = -0.29). The second component described areas with high percentage cover of large trees (r = 0.86) and low percentage ground-cover (r = -0.49). These two components were used in the logistic habitat model.

Large (4 – 6 cm wide carapace) *Ocypode* (ghost) crabs shared both the mudflat and beach with Malaysian plovers. Previous studies suggested that *Ocypode* crabs depredate plover eggs and chicks (Watts and Bradshaw, 1995; Gregory-Smith, 1998). Thus at each sampling section I recorded the number of *Ocypode* burrows (diameter greater than 5 cm) in three randomly selected 12 m^2 quadrats on the beach.

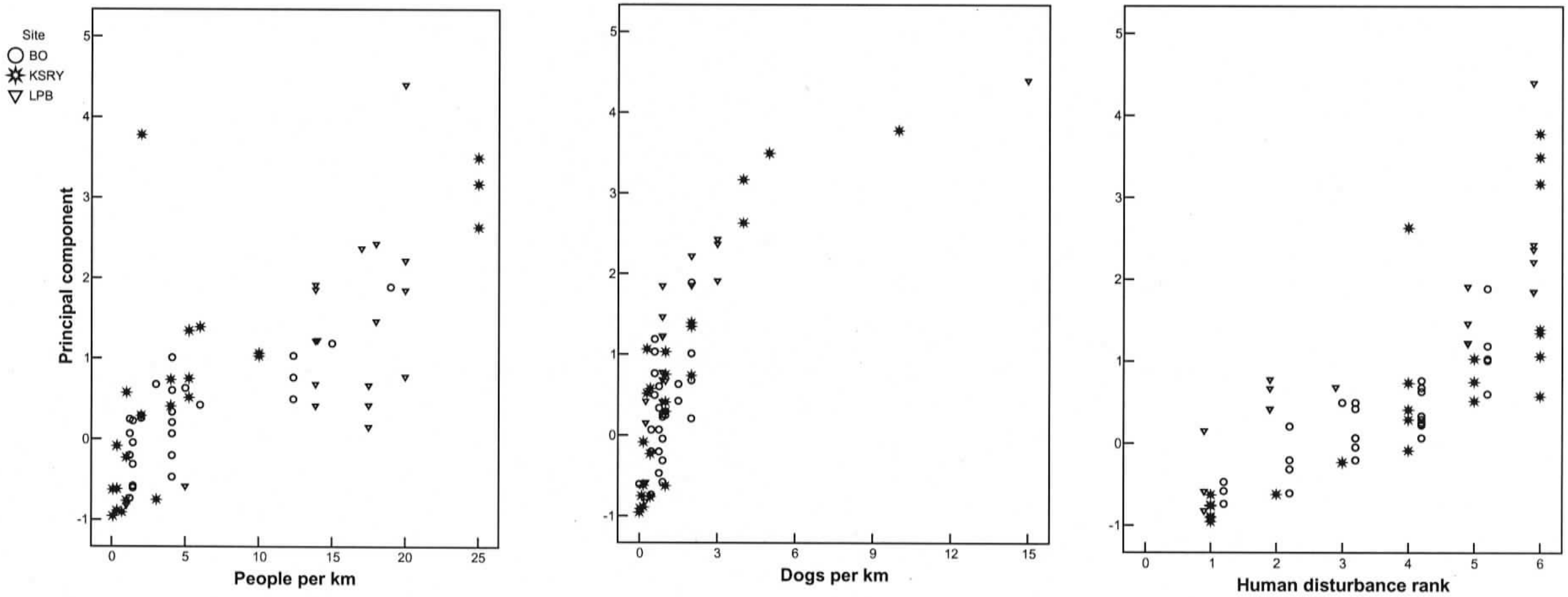
Small *Scopimera* (bubbler) crabs are a major prey item for Malaysian plovers (Yasué. M. unpublished data). At each sampling section, I measured the width of the mudflat where crab burrows were present. I paced the mudflat and visually estimated the proportion of the area with high, medium or low crab densities. These proportions were used to calculate weighted average crab densities for the section. At each of the three density categories I counted all burrows that had a 2 to 10 mm diameter in two 0. 46 m2 randomly placed quadrats. I then multiplied the width of the mudflat with weighted average burrow densities to calculate a crab abundance estimate for the sampling section. Crab sampling was conducted between 08:00 to 13:00 at 0.7 to 1.0 m (based on published tide table values) on 15 to 25th July of 2004 and 2005. Although direct *Scopimera* counts would have yielded more accurate estimates of prey availability than burrow counts, my method was necessitated due to the large number of sites that needed to be sampled over a short period. Moreover burrows were a good indicator of crab availability because crabs created burrows at every low tide period to feed at the surface (Takahashi et al., 2001).

I counted people and dogs on the mudflat, beach or up to 20 m in the vegetation behind the beach along 500 to 800 m long sample sections. These counts were standardized to an average number of people or dogs per km at each site. Repeated counts were conducted at sampling sections on different, times, days and month (*n* = 9 to 29 per sections). Census sections were larger than 200 m because people frequently walked or drove along the length of the beach and using 200 m would have yielded many zero counts, making comparisons between breeding territories difficult.

Human visitation rates are likely to increase dramatically in tourist areas during Thai holidays and in less tourist-oriented areas during short-term periods of high fish stocks. Maximum rather than average human visitation may be important for plover breeding success. This may not be adequately quantified by random counts. Consequently I also qualitatively ranked the human disturbance level within a 500 m radius of each nest site based on the number of houses, restaurants, hotels, roads, shrimp ponds, trails or other man-made structures. Scrubland with no human use was ranked 0, and areas with interconnected resorts and paved roads were ranked 5.

I used a factor analysis to reduce these three correlated human disturbance variables (*Pearson's* $r = 0.33 - 0.54$) into one variable for each year that accounted for 69 and 61 % of the variation. All three variables were positively correlated to the principal component (Component's matrix factor loadings 0.69 to 0.85, Figure IV-1).

2004


Site
BO
KSRY
LPB
Principal component
-1
0
1
2
3
4
5
0
5
10
15
20
25
People per km
0
3
6
9
12
15
Dogs per km
0
1
2
3
4
5
6
Human disturbance rank

2005

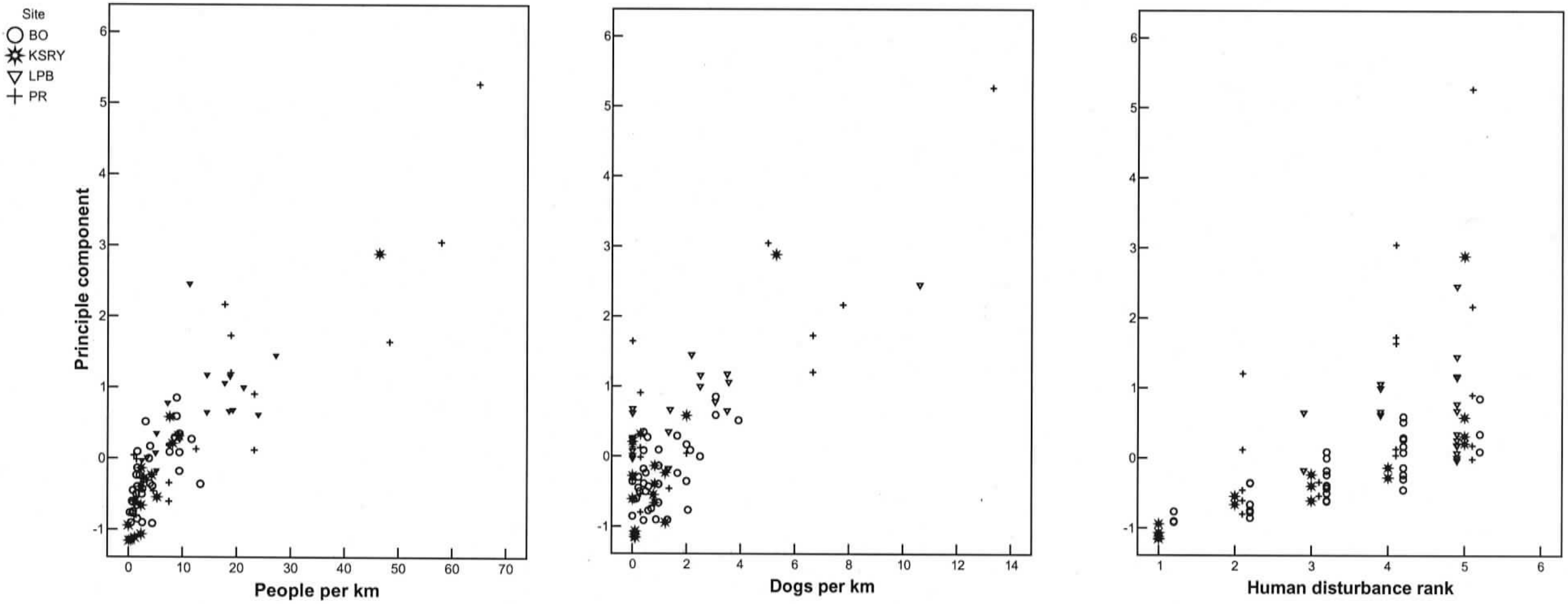


Figure IV-1 Human disturbance principal component.

Scatter plots showing the relationship between instantaneous human (left) and dog (middle) counts and qualitative human disturbance ranking (right) to the human disturbance principal component for 2004 (top) and 2005 (bottom). Although human disturbance rankings were integers, I displaced the x-axis by 0.1 or 0.2 so that so that it is easier to differentiate the site symbols on the graph.

a) Habitat selection model

To identify factors influencing territory selection, I compared the habitat characteristics of beach breeding territories to control sections without nests in the four areas (n = 2004 and 2005, breeding : control sections 55 : 36 and 79 : 40). Control sites were selected based on proximity to nest sites and interspersed among nest sites as much as possible to avoid spatial autocorrelation (Legendre, 1993). All beach sections without nests that were immediately adjacent to nesting territories were included as control sites. To increase sample size of control sites, other beach sections that were within 2 km of nest sites were also included in my study.

Control sites were visited at least once per month from January to July to ensure that there were no breeding plovers. I did not conduct more frequent checks at these sites because Malaysian plovers generally occupied territories at least one month prior to laying a clutch and usually did not change habitats after a failed nesting attempt. The variables that were included in the habitat selection models were: beach width, the percentage cover of small, medium and tall vegetation behind the beach, *Ocypode* burrow densities, *Scopimera* burrow abundance, the human disturbance factor, and site. As discussed above, in 2005 two principal components were used instead of direct vegetation cover behind the beach and percentage cover of beach vegetation was also included in the analysis. For all independent variables I checked the variable inflation factor (all < 2), tolerance (all > 0.5) and bivariate Pearson's correlation coefficients (all < 0.5) to ensure there was no multicollinearity in the data set.

b) Breeding success model

To minimise pseudoreplication, I calculated reproductive success per breeding territory for each pair of plovers rather than by each breeding attempt. Thus for pairs renesting during a season, the habitat characteristics for successive breeding attempts were averaged and the number of chicks hatched or fledged was summed and then divided by the number of breeding attempts per pair. I used these measures of breeding "efficiency" rather than total eggs hatched or chicks fledged because additional breeding attempt in a season could entail costs to adult survivorship (Ghalambor and Martin, 2000).

In the breeding success models I identified habitat characteristics that influenced the number of chicks hatched per breeding attempt and the number of chicks fledged per breeding attempt (n_{pairs} for hatch success 2004, fledge success 2004, hatch success 2005 = 49, 49, 71).

I tested the same variables as in the habitat selection model and also included conspecific nest density because if there are density-dependent declines in breeding success, these indirect effects may lead to a greater combined impact on populations, than could be attributed to the direct effects of habitat loss alone (Sutherland and Norris, 2002). Also, a previous study on Kentish plovers suggested that more nests were predated in areas with higher nesting densities (Page et al., 1983). The nest density estimate was the number of conspecific nests within 200 m of the nest, based on UTM coordinates obtained at each nest.

For the habitat selection, hatch and fledgling success analysis I used binary logistic regression and selected the most important variables using log-ratios stepwise backwards elimination (removal if $P > 0.10$) in SPSS version 11.0 while controlling for site. The dependent variable for the habitat selection model was the presence or absence of nesting plovers. For breeding success, I recoded the number of chicks hatched and fledged per breeding attempt of a pair into high and low categories that had approximately equal sample sizes (high categories for hatch 2004, fledge 2004, hatch 2005 were: eggs hatched / clutch >= 1.5, chicks fledged / clutch >= 0.67, eggs hatched / clutch >= 1, chicks hatched / clutch >= 0). Although scoring breeding success reduces resolution, this was necessary because data could not be transformed into a normal or a Poisson distribution using standard data transformation techniques. I conducted analysis for the two years separately because different independent variables were tested between these years (i.e. percent beach ground-cover in 2005 and factors instead of raw data for vegetation structure in 2005).

To check for the independence of successive nesting territories or control sites I ordered the 200 m beach sections (south to north) within each site and used scatter plots, runs test and lag-1 autocorrelation functions to quantify the degree of serial autocorrelation in the residuals of my model (Pindyck and Rubinfeld, 1998; Keitt et al., 2002; Diniz-Filho et al., 2003). Data showed no sign of strong spatial autocorrelation (significance values for the runs test and autocorrelation functions were all > 0.05)

3) Nest and brood disturbance observations

In 2004 and 2005 I conducted 70 and 193 hours of observation on incubating birds and 32 and 77 hours of observations on broods from either a hide or by sitting on the mudflat more than 150 m from the beach. Between the two years, the observations were conducted on 108 and 54 different nests and broods. All error bars here and throughout represent standard errors. Incubation watches lasted 1 to 2 hours (mean length 75.7 ± 2.3 minutes, n = 211) and brood watches lasted 45 minutes to 1 hour (mean length = 50 ± 1.3 minutes, n = 134). Behavioural observations were conducted at random times throughout the day between 6:30 to 17:30. During incubation watches I continuously observed the nests and recorded the total amount of time incubating birds were flushed off nests due to disturbances. Disturbances times during brood watches were measured from the time when the first adult began responding to a disturbance until the last adult stopped. When one of the adults led the chicks into the vegetation behind the beach during disturbances, I was only able to measure the end time of the disturbance based on the behaviour of the adult remaining on the beach. However, in most cases, soon after the beach adult stopped disturbance behaviour, the adult that was in the vegetation returned to the beach. One of the adults was always visible during disturbance observations. Birds were considered disturbed if they were exhibiting anti-predatory behaviour such as neck out-stretched vigilance posture, flushing onto the mudflat, "rat-running", chasing intruders, calling to distract predators, false brooding or crouching (Gochfeld, 1984). If multiple nest or brood observations were conducted on the same pair, these values were averaged for subsequent analysis.

Results

1) Monitoring of breeding pairs

Productivity

Overall productivity at the three sites was higher in 2004 (1.08 ± 0.15) than in 2005 (0.53 ± 0.11 chicks fledged per pair). Mayfield stage survival estimates for 2004 egg/chick and 2005 egg/chick (survival, n_{nests}) 0.61 ± 0.06, 86 / 0.51 ± 0.7, 56 and 0.39 ± 0.05, 116 / 0.53 ± 0.06, 64 (Mayfield, 1961).

Twenty nests were inundated by tides and 15 nests trampled (2 by cows, 11 by construction vehicles, 2 by motorbikes) (Figure IV-2). I attributed predation to be the cause of failure for 26 nests. For most of these suspected predations, entire clutches disappeared between checks. I was unable to determine the predator type.

In almost all chick mortalities I was not able to find carcasses nor determine the cause of death. One chick in a heavily disturbed site was found trampled in a human footprint, and four other chicks were found within 1 m of the nest with no apparent physical damage. Adults remained in territories after chicks had disappeared and so I was confident that chicks had died, rather than moved to different habitats.

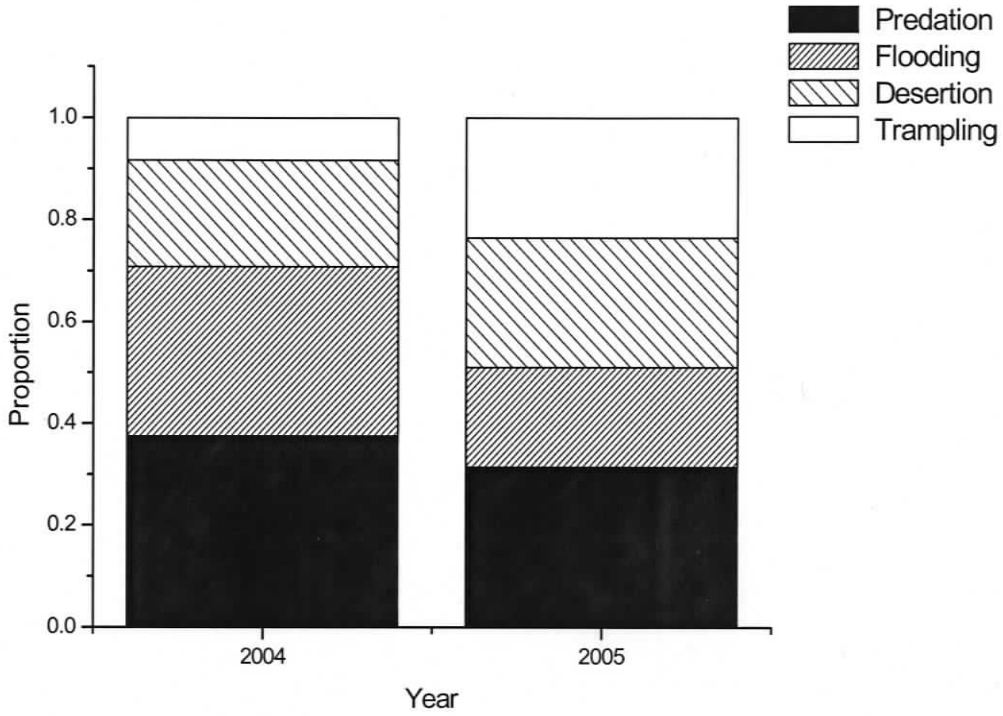


Figure IV-2 Causes of nest failure.
26 and 60 Malaysian plover nests failed in 2004 and 2005.

2) Habitat model

a) Habitat selection model

In both years plovers selected wide beaches that had a low percent cover of tall vegetation backing the beach and low human disturbance (Table IV-1, Figure IV-3). In 2005, birds also appeared to select beaches with a low percentage cover of beach ground-cover . In 2004 it also appeared that plovers may be selecting areas with high percent cover of medium vegetation height, however this result was not statistically significant (*P* = 0.075).

Table IV-I Habitat model – nest presence.
Results of a binary logistic model predicting the presence of Malaysian plover nests within 200 m beach sections in the Gulf of Thailand (*n* = 2004 and 2005 breeding : control section 55 : 36, 79 : 40).

	Habitat Selection					
	2004			2005		
Variables	*b*	Wald	*P*	*b*	Wald	*P*
Site		5.5	0.066		5.4	0.144
Human disturbance factor	-2.88	8.0	0.005	-0.734	3.9	0.049
Beach width (m)	0.64	14.5	< 0.0001	0.067	4.8	0.029
Tall vegetation (% cover)	-0.057	4.8	0.028	-0.78	6.8	0.009
Medium vegetation (% cover)	0.037	3.2	0.075	n.s.		
Beach ground-cover (%)	n/a			-6.02	7	0.008
Model χ^2	55.1			45.7		
df	6			7		
P	< 0.0001			< 0.0001		
Area under ROC curve	0.932			0.835		

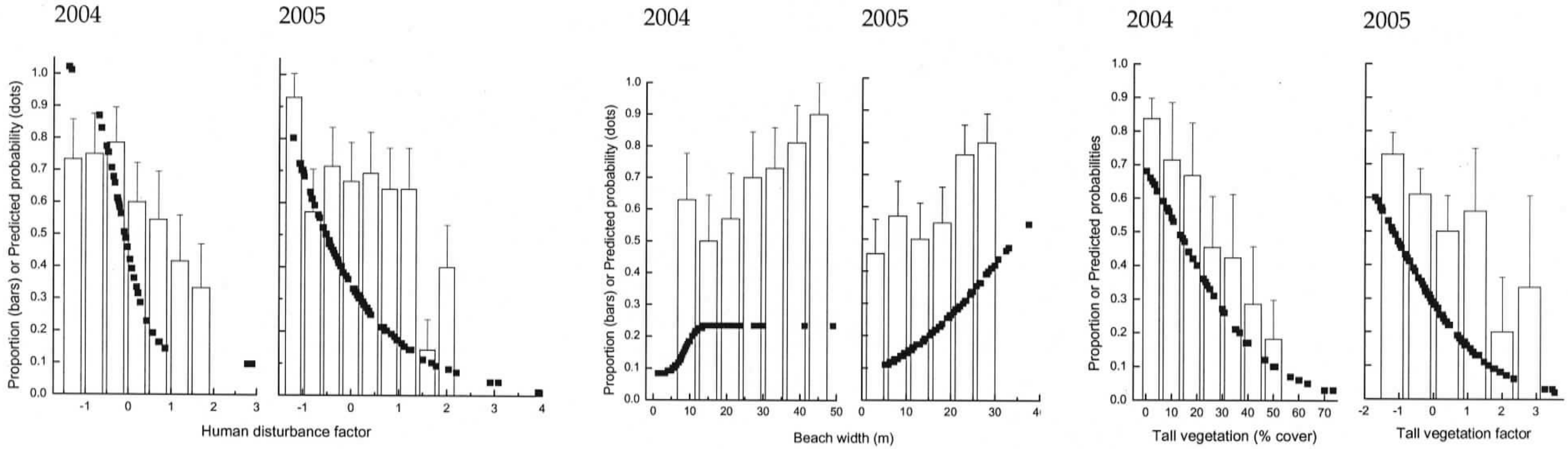


Figure IV-3 Factors influencing habitat selection.
Variation in the proportion of beach sections with or without Malaysian plover nests in relation to (left) human disturbance (middle) beach width and (right) tall vegetation cover backing the beach (factor in 2005) in 2004 (left) and 2005 (right). For the highest independent variable category in each graph, I pooled all higher values so that there was sufficient sample size in each bar ($n > 5$). Binomial error bars are shown. Black dots represent fitted logistic regression curve showing the predicted probabilities from the model. For this curve, the other significant independent variables were set to mean values. The bar graph and the logistic curve are plotted on the same scale.

b) Breeding success model

In 2004 plovers were more likely to hatch chicks at least 1.5 chick per clutch in areas with low Ocypode burrow densities, low conspecific density, and low human disturbance (Table IV-II, Figure IV-4). Ocypode burrow density and conspecific nest density both also affected the likelihood of hatching at least 1 chick per clutch in 2005.

Table IV-II Habitat model – breeding success.
Results of a binary logistic model predicting the number of Malaysian plover chicks hatched per clutch (n_{pair} for 2004 and 2005 = 49, 71).

	Chicks hatched / clutch					
	2004: likelihood of >= 1.5			2005: likelihood of >= 1		
Variables	*b*	*Wald*	*P*	*b*	*Wald*	*P*
Site		2.51	0.284		3.3	0.347
Conspecific density (pairs within 200 m)	-0.79	3.9	0.047	-0.61	4.2	0.04
Ocypode burrow density	-5.6	6.7	0.009	-4.5	9	0.003
Human disturbance	-1.71	5.5	0.021	n.s.		
Model χ^2	18.2			18.9		
Df	5			5		
P	0.003			0.002		
Area under ROC curve	0.795			0.79		

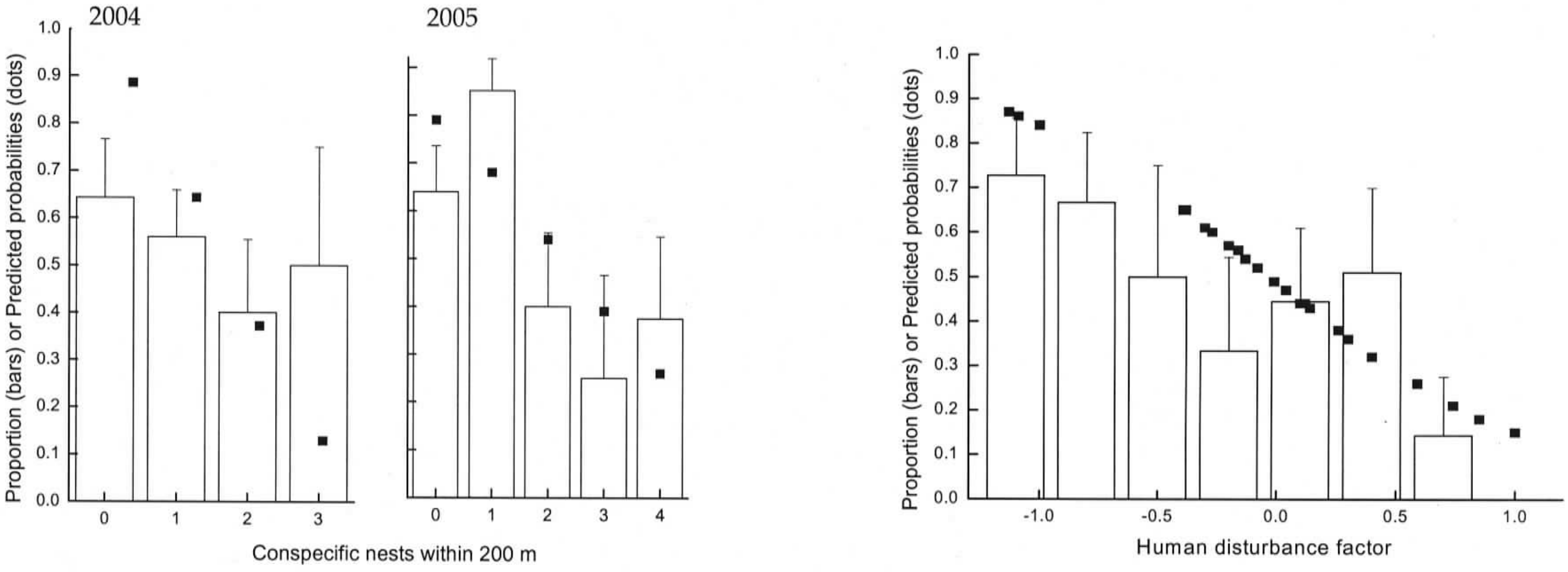


Figure IV-4 **Factors influencing hatch success.**

The effects of (a) conspecific nesting density and (b) human disturbance on the proportion of Malaysian plovers that hatched at least 1.5 and 1.0 chicks per clutch in 2004 and 2005 respectively. Black dots represent fitted logistic regression curve showing the predicted probabilities from the model. The bar graph and the logistic curve are plotted on the same scale.

In 2004 the probability of fledging at least 0.67 chicks / clutch was greater in areas with a high percent cover of medium vegetation ($b = 0.084$, *Wald* = 7.6, $P = 0.006$, model $\chi^2 = 18.1$, df = 5, $P = 0.003$, AUC = 0.79, Figure IV-5). The data suggested that conspecific density may influence fledge success rates, however this was not statistically significant ($b = -0.654$, $P = 0.095$). In 2005, none of the habitat variables predicted the likelihood of fledging more than 0 chicks per clutch (Model $\chi^2 = 7.54$, df = 4, $P = 0.11$).

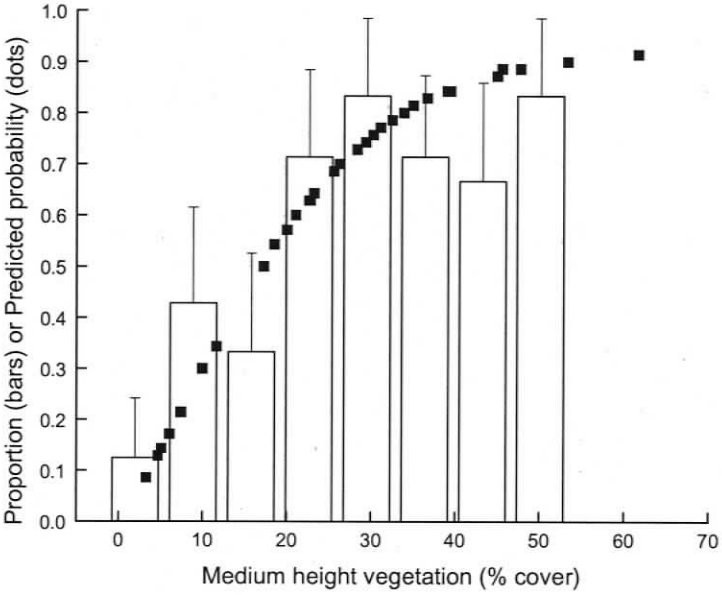


Figure IV-5 Factors influencing fledeling success.

The effect of percent cover of vegetation of medium height on the proportion of Malaysian plovers that fledged at least 0.67 chicks per clutch in 2005. Black dots represent fitted logistic regression curve showing the predicted probabilities from the model. The bar graph and the logistic curve are plotted on the same scale.

3) Nest and brood disturbance observations

Overall during both incubation (211 observation on 108 pairs) and chick-rearing (134 observations on 54 pairs), adults spent very little time responding to anthropogenic and natural disturbances (Incubation: 3.2 % of total time, chick-rearing 10.1 %). Between the two years only 49 and 44 pairs showed any disturbance responses in 2004 and 2005. The majority of anthropogenic disturbances were people, dogs, cattle or motor vehicles on the beach. Anthropogenic disturbance rates were very low and there were very few people and dogs in the breeding areas (5.2 ± 0.7 people/km and 1.4 ± 0.3 dogs/km for nesting territories). Natural causes of disturbance included potential predators such as ghost crabs, mongoose, peregrine falcons, attacks from neighbouring conspecifics, as well as false alarms (**Figure IV-6**).

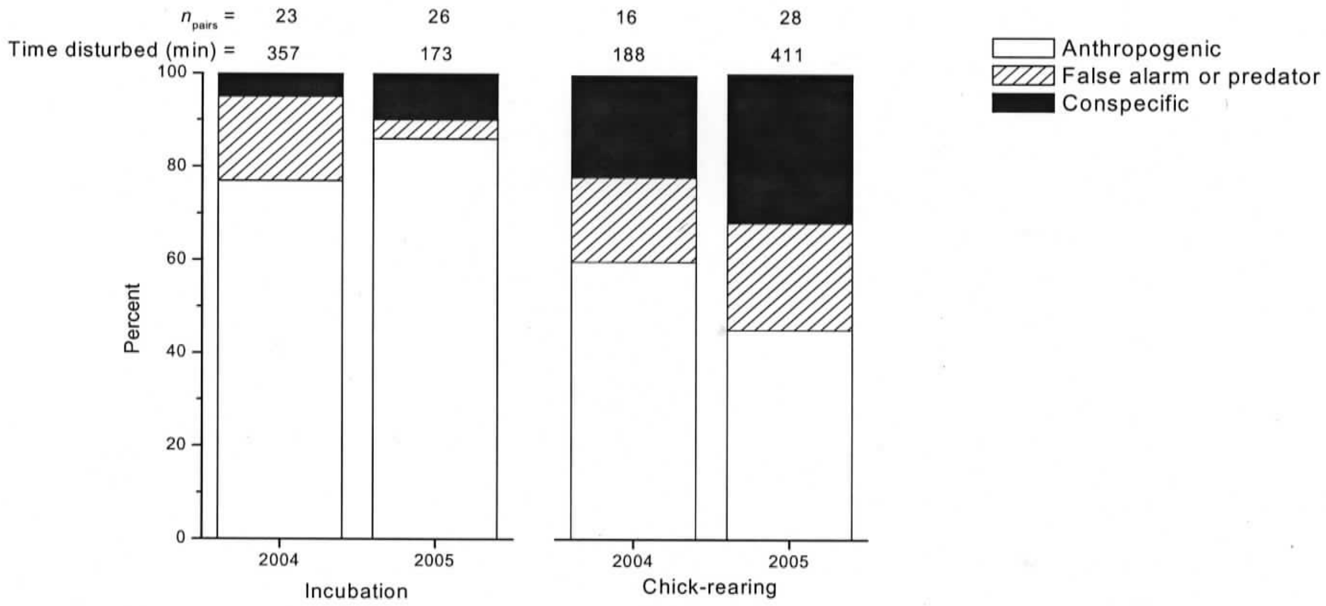


Figure IV-6 Response to disturbances.
The proportion of time Malaysian plovers spent responding to different types of disturbances during incubation and chick-rearing.

a) Predators

In 372 hours of observation I observed no mortalities due to predation. The only potential avian predator observed were three peregrine falcons that were hunting other shorebirds. I also saw small Indian mongoose (*Herpestes javanicus*) near nests and on one of these occasions I observed an adult successfully lead a mongoose away from its nest. On 10 occasions I observed *Ocypode* crabs apparently attempt to capture chicks or eggs. The most significant single source of natural disturbances for chick-rearing adults (30 % of natural disturbances) were collared kingfishers (*Halcyon chloris*) that were feeding on large fiddler crabs (*Uca annulipes, Uca vocans*) on the mudflats. It was unclear whether these kingfishers actually posed a true threat to chicks because I did not see kingfishers attack chicks. However *Halcyon* kingfishers are opportunistic predators that occasionally feed on other birds (Woodall, 2001).

b) Responses to disturbances

During false alarms, anthropogenic, conspecific or mammalian predator disturbances, adults quickly lead chicks into the vegetation behind the beach. The chicks remained still in the vegetation, while one or both of the adults returned to the beach to monitor and distract the predators. Similar behaviour have been demonstrated in disturbance responses for other *Charadrius* plovers (Gochfeld, 1984; Weston and Elgar, 2005a). Eventually, the chicks would usually resume feeding within the vegetation and then progressively move to the beach and then eventually to the mudflats. Plovers also crouched when responding to avian predators, or false alarms caused by species such as white-bellied sea eagles or osprey.

Discussion

Sandy tropical beaches are under tremendous development pressure. This study suggests that development on Thai beaches can reduce both habitat availability and breeding success for Malaysian plovers. Malaysian plovers share several habitat requirements with related temperate *Charadrius* plovers (Flemming et al., 1988; Powell, 2001), and they are similarly vulnerable to human disturbance, changes in vegetation cover, or reductions in beach width. Although numerous studies have examined these impacts on temperate environments, this is the first detailed study demonstrating the potential impacts of coastal development on a tropical *Charadrius* plover. Moreover, tropical species (and in particular species in Southeast Asia) may be even more vulnerable to development because of weaker conservation regulations in many of these countries (Kontogeorgopoulos, 1999).

Human disturbance

In 2004, human disturbance affected both habitat availability and hatch success. This is one of the first studies demonstrating the effects of human disturbance on a breeding tropical wader. Clearly nest monitoring showed that trampling and construction affected hatch success (Liley, 1999; Ruhlen et al., 2003). Trampling may be exacerbated by reduced beach width because plovers may be forced to nest on footpaths, cattle routes or motorcycle pathways. In LPB where a seawall was being constructed, birds repeatedly nested on the dirt road for construction vehicles because the rocky boulders of the seawall replaced most of the sandy beach.

Previous studies showed that human disturbance may affect hatch success by forcing adults off nests, thereby making eggs more vulnerable to opportunistic predators such as gulls (Bolduc and Guillemette, 2003). Diurnal nest predation was probably not a significant causative factor, because I observed few opportunistic predators. However, it is possible that predation may be an important mechanism at night because there were many fishers on the beaches during this time. People dig for *Ocypode* crabs on beaches near Malaysian plover nests. Moreover, these crabs are more active at night when they may pose a much greater threat (Watts and Bradshaw, 1995).

Heat stress may be an important mechanism linking human disturbance levels and productivity. Malformations and embryo mortality begins to occur at 40.5 C^0 in some birds (Webb, 1987) and a concurrent study at this field site showed that egg temperatures can rise above this temperature after only a few minutes of exposure to the sun (M. Yasué, unpublished data). Thus even at the very low levels of disturbance at my study site, embryo survival may be reduced (Lundy, 1969). Although there have been few studies on human disturbance and heat stress on plovers, Weston & Elgar (2005) suggested that reduced brooding due to human disturbance may have resulted in lower fledgling success for the Hooded plover *Thinornis rubricollis* in Australia.

Twenty-three percent of failed nests were caused by desertion. This may be partly attributed to human disturbance. Adults may chose to abandon nests if they are constantly forced off nests on a hot day and embryo survival seems unlikely. Alternatively, as waders probably perceive people as predators (Frid and Dill, 2002; Beale and Monaghan, 2004b), constant disruption by people may make adults perceive a greater personal risk to incubation and increase the likelihood of desertion (Ghalambor and Martin, 2001).

Beale & Monaghan (2004) showed reductions in reproductive success in seabirds disturbed by people. As with my study, the mechanism causing reduced breeding success was difficult to identify because birds spent very little time overtly responding to human disturbance. Stress and physiological responses such as increased heart rate, which are not detectable by observations, may contribute to lower adult body condition, lower adult attendance, or greater nest desertion leading to reduced breeding success (Beale & Monaghan 2004).

Human disturbance had no effect in 2005 on breeding success. This may be attributed to the presence of one or two effective wide-ranging predators such as a mongoose on two very undisturbed beaches in KSRY in 2005. Thirty-five and 40% of the nests monitored in 2004 and 2005 were on these beaches. In 2005, 16 nest of these nest were predated, whereas only 5 were predated in 2004. Also in 2005, my methods may have underestimated the amount of human disturbance perceived by birds at the construction sites. Although I counted more people on these beaches compared to 2004, birds may have perceived an even greater predation threat because of the presence of large, noisy machinery.

Fledging success was not affected by human disturbance. Although Malaysian plover chicks may be occasionally trampled by people or motor vehicles, in previous temperate research, the main mechanism causing reduced chick survival in heavily disturbed areas is the reduction of chick feeding time (Flemming et al., 1988; Piatt et al., 1990; Lord et al., 1997). Chick starvation risk may be less important for Malaysian plovers because of the relatively low human disturbance rates at my study site, the more consistent prey base in the tropics, and the lower feeding requirements due to the warmer weather (Martin, 1996). Moreover there may be little remaining variability in human disturbance to detect differences in fledgling success because human disturbance already affected habitat selection and (in 2004) hatch success.

Conspecific nest densities

In both years, breeding success was lower in areas of high conspecific nesting density. This may be due to greater predation risk (Page et al., 1983) or direct infanticide by neighbouring adults (Fraga and Amat, 1996). Alternatively, in areas with high nesting densities, adults may spend more time defending territories, leaving the chick more vulnerable to predation or heat stress. If habitats are lost due to tourism development, birds may be forced to nest in higher densities in remaining areas and suffer lower breeding success until population sizes are reduced to match the lower habitat availability (Goss-Custard et al., 1995). In LPB, approximately 80% of the habitat was lost due to the construction of the seawall. In 2005, the mean nearest nest distance for this site was only 30.4 ± 3.89 m (n = 6), as compared to 604 ± 159 m for all other sites combined and 190.6 ± 25.6 m (n = 9) at the same site in 2004.

Changes in habitat structure

Beaches backed by vegetation of medium (0.5 - 5 m) height (*Acacia* and mangroves) appeared to provide better nesting habitat than beaches backed by tall vegetation (*Casuarina* pine trees). Although there were very few raptors observed in the breeding season, migrating peregrine falcons and sparrowhawks (*Accipiter spp.*) were frequently observed during the non-breeding season (DeCandido et al., 2004) and may thus still influence plover habitat selection in the breeding season. During chick rearing, *Acacia* and mangrove bushes appeared to be an important hiding and foraging habitat for chicks (Clark and Nudds, 1991). In areas with high disturbances, chicks fed mainly within the vegetation or along the beach close to the vegetation, instead of on the mudflats (Liley, 1999; Weston and Elgar, 2005a). These bushes also provided shade for chicks when adults were not able to shade chicks during adult feeding bouts and disturbances (Visser and Ricklefs, 1993; Weston and Elgar, 2005a).

Significance and management implications

My study suggested that there has been a rapid decline in available beach habitat for the Malaysian plover in Prachuap Khiri Khan and Petchburi provinces in the Gulf of Thailand. This is a concern because, as far as I know, this study was conducted on the largest plover population and least disturbed breeding habitat in Thailand. It is likely that the impacts of tourism are much greater for the small populations that may continue to exist in small, undisturbed pockets within more tourism-oriented beaches throughout Thailand. In a concurrent study I interviewed ornithologists and visited numerous beaches on both coasts of Thailand to census Malaysian plovers (M. Yasué, unpublished data). Almost all the beaches where plovers bred less than ten years ago were now highly developed tourist areas with no plovers.

Well-managed protected areas, which do not allow habitat conversions and limit the number of people on beaches, may help conserve plover populations by increasing the amount of available breeding habitat and potentially reducing nesting densities. The habitat model suggests that beach width, tree heights, *Ocypode* crab densities and human disturbance rates should be considered when selecting areas for protection. In terms of management of these protected areas, sign-posted fencing around beach areas where plovers breed (Lord et al., 2001) may reduce human access during periods when birds are most sensitive to disturbance, such as in the hottest months of April and May. Moreover in key Malaysian plover breeding areas, tall trees could be removed, or beach height could be artificially raised to create more suitable habitat (Ziewitz et al., 1992; Round et al., 2004).

However, with continued rapid tourism growth, ineffective land-use planning and strong government support for tourism (Kontogeorgopoulos, 1999; Kontogeorgopoulos, 2004) these types of recommendations are unlikely to be implemented in Thailand. Part of the KSRY and PR sites are in protected areas, and at present there is little tourism development in these areas and relatively few changes occurred during 2004 and 2005. However, protected area status in Thailand does not necessarily preclude development (Dearden and Chettamart, 1997). In 2004 and 2005, land speculators visited the most important waterbird breeding habitat within the protected area of KSRY. In many protected areas, managers may be more interested in generating revenue through tourism development than in meeting conservation goals. Moreover, on beaches within protected areas, cleaning vehicles regularly run along the beaches sweeping up garbage and destroying potential nests of breeding waders (C. Chettamart, National Park Superintendent, unpublished data). In the few protected areas that actively discourage development there are still no active habitat restoration projects or exclosures (Chettamart, C. unpublished data).

Conclusion

This study demonstrates the value of using multiple approaches including habitat modelling, nest monitoring and behavioural observations to evaluate and interpret the effects of habitat loss and human disturbance on a tropical wader population. By examining a series of habitat variables relating to predation risk and prey availability, I was able to identify important habitat characteristics for the Malaysian plover and assess how anthropogenic changes may influence habitat suitability. I was also able to evaluate possible direct links between human disturbance and changes in habitat structure and productivity, by conducting behavioural observations and assessing causes of nest failure.

My demonstrates the importance of conducting conservation-related studies on tropical beaches (Martin, 1996; Brown and McLachlan, 2002; Fish et al., 2005). Differences in climate and environment can affect both the natural constraints on breeding and vulnerabilities to different types of anthropogenic change. Many tropical countries have similar conflicts between tourism and conservation and there are several red-listed beach-nesting species such as the

Chinese-crested terns *Sterna bernsteini* Schlegel or green turtle *Chelonia mydas* L. (Hall and Page, 2000). In Thailand, little terns *Sterna albifrons* and red-wattled lapwing *Vanellus indicus* Boddaert breed alongside Malaysian plovers. Multi-species studies could also help to determine cumulative impacts of tourism development on wildlife (Root et al., 2003).

In regions where there is a paucity of ecological research such as Southeast Asia, this type of behavioural approach may be an effective means to rapidly acquire data that has greater generality than site-specific monitoring studies and requires shorter study periods than demographic studies (Sutherland, 1998c). Although current policy barriers restrict the conservation value of this study, I hope that the methods used may have value for other regions with similar environments, threatened beach wildlife and a more favourable socio-political climate for wildlife conservation.

V. The effects of heat stress, predation risk and parental investment on Malaysian plover nest return times following a human disturbance

Yasué, M. and Dearden, P. 2006. Biological Conservation 132: 472-480

Abstract

Shorebirds leave nests and conduct distraction displays when approached by people. The time taken for shorebirds to return to nests depends on numerous factors that affect the costs and benefits of incubation and anti-predator behaviour. Understanding this trade-off may help assess the reproductive consequences of different nest return times and identify variables to consider in breeding disturbance studies. I subjected 73 Malaysian plover (*Charadrius peronii*) nests to standardized human disturbances and an analysis of covariance was used to determine how weather, time of day, embryonic age, weeks into breeding season and nest attendance (proportion of time adults incubated nests) influence nest return times. Egg temperatures were estimated using a regression model that predicted the temperature inside unshaded eggs from air temperature, cloud cover and time of day (r^2 = 0.88). I assessed the relationship between nest return times and hatch success. Plovers returned to nests faster at higher modeled egg temperature ($P = 0.010$), in the morning ($P = 0.003$), if they had younger clutches ($P = 0.038$), and if they had high nest attendance prior to the disturbance ($P = 0.015$). Pairs that returned to nests faster had lower hatch success ($P = 0.021$). This may be because pairs that spend more time distracting humans may also spend more time distracting predators. These results suggest that short nest return times may not indicate low fitness costs of disturbance. The thermal and predation environment in addition to nest return times should be taken into account when assessing the deleterious effects of human disturbance.

Introduction

An animal's response to a person depends on both the extent of the perceived threat as well as the possible fitness consequences of the response (Frid and Dill, 2002; Peters and Otis, 2004; Yasué, 2006a). Although many researchers have examined how the perceived threats (e.g. people running versus walking) affect behaviour (Lord et al., 1997; Thomas et al., 2003b), few studies have assessed how costs to adult survivorship or productivity influence responses (Stillman and Goss-Custard, 2002; Beale and Monaghan, 2004a) and even fewer have examined this in breeding birds (Beale and Monaghan, 2004b).

With more people visiting beaches, beach-nesting shorebirds may be increasingly vulnerable to adverse impacts of human disturbance (Burger, 2000; Lord et al., 2001). A better understanding of the trade-offs that shape the response of breeding shorebirds to human "predators", may elucidate the relationship between the observed behavioural responses of wildlife to people and reproductive costs (Gill et al., 2001b). This may help managers identify locations, times or populations in which human disturbance may be most likely to affect shorebird survivorship or productivity (Weston and Elgar, 2005a).

Temperature regulation of clutches by parental incubation or shading is a key factor affecting hatching success (Webb, 1987). However, when people approach small shorebird nests (*Charadriidae* and *Scolopacidae*), adults will often leave the nest and attempt to lead people away with conspicuous behaviours such as calling, feigning injury, "rat-running" or false-brooding (Gochfeld, 1984). Eventually the parent will return to the nest discreetly to avoid leading a predator to the nest (Weathers and Sullivan, 1981). This study examines factors influencing the time taken for a ground-nesting tropical shorebird, the Malaysian plover (*Charadrius peronii*), to return to a nest after a standardized human disturbance ("nest return times").

Nest return times are influenced by numerous physiological, ecological and environmental factors that affect the risks and rewards of anti-predator responses. Birds will return to nests faster if there is a high risk of mortality for unattended nests (Montgomerie and Weatherhead, 1988). In tropical environments where ambient temperatures frequently rise above 41 ^{0}C, mortality of embryos can occur in exposed (not shaded by parents) clutches (Bennett and Dawson, 1979; Webb, 1987; Stoleson and Beissinger, 1999).

The type and density of natural predators may also influence optimal return times (Montgomerie and Weatherhead, 1988; Brunton, 1990). Shorebirds may prolong nest return times if there are visual predators such as corvids that can follow shorebirds back to the nests (Weathers and Sullivan, 1981; Martin et al., 2000). Alternatively, if the predominant predators are hedgehogs (Jackson, 2003) or snakes (Weatherhead and Blouin-Demers, 2004) that rely less on visual cues or are opportunistic and hunt only unattended nests, then short nest return times may yield higher hatch success (Bolduc and Guillemette, 2003). Shorebirds may also adjust the length of time engaged in distractive displays because the efficacy (Byrkjedal, 1987) and potential risks may differ among predators (Montgomerie and Weatherhead, 1988).

Parents may also invest more time or energy defending more valuable, older clutches, and thus take a longer time to return to the nest (Montgomerie and Weatherhead, 1988; Brunton, 1990). This age effect on return times may be moderated by the greater vulnerability of exposed older clutches to heat stress than younger clutches (Dawes, 1979; Webb, 1987). Birds may also exhibit stronger parental care for clutches later in the breeding season because they have fewer opportunities to renest within the season and recoup the costs of clutch failure (Barash, 1980; Parish et al., 1997).

Nest return times may also depend on individual nest site (Montgomerie and Weatherhead, 1988) or parental qualities (Conway and Martin, 2000; Gorman and Nager, 2003). For example, nest location could affect the incubation requirements of the developing embryo (Walsberg and King, 1978; Amat and Masero, 2004a) and predation risk around the nest (Howlett and Strutchbury, 1997; Martin et al., 2000) . Parental qualities that can influence anti-predation tactics include the body condition of the parent (Hegyi and Sasvári, 1998; Dearborn, 2001), as well as previous breeding experience (Montgomerie and Weatherhead, 1988) or habituation to people (Nisbet, 2000).

A bird with high nest attendance (the proportion of time the nest is incubated by either parent) prior to the standardised disturbance may also be likely to quickly return to nests after a disturbance. This is because attendance is influenced by many of the same factors discussed above that shape nest return times (i.e. clutch incubation requirements, parental body condition). Consequently among nests, the individual nest variability in return times are likely to correlate, at least partly, to patterns in nest attendance. For this reason I included nest attendance in my predictive model of nest return times to capture part of the variability in return times due to individual site or parental characteristics.

In the first part of this study the effects of egg temperature, embryonic age, days into the breeding season, and nest attendance on nest return times were examined. Egg temperature was modeled based on shaded air temperature, cloud cover and time of day, using a thermocouple to predict the temperature inside an exposed similar sized and coloured quail egg. To interpret the anti-predation behaviour of these plovers and identify predators as well as other sources of disturbances, I monitored causes of nest failure and conducted diurnal predator and disturbance surveys.

The fitness outcomes of different parental anti-predator decisions may depend on physiological or environmental factors that influence the vulnerability of exposed clutches to thermal stress as well as ecological factors such as predation that influence the benefits of distraction displays (Yasué, 2006a). In the second part of this study, I examined the relationship between nest return times and hatch success. Previous studies often inferred fitness consequences based on the extent of these behavioural changes without directly measuring changes in productivity or survivorship (Rodgers and Schwikert, 2002; Thomas et al., 2003b). In this study I assessed the validity of this approach and also identified conditions in which responses of shorebirds to people could reflect potential costs to fitness.

Methods

Study species

Malaysian plover (*Charadrius peronii*) were selected for this study because previous studies indicated that human disturbance reduces breeding success in related *Charadrius* species (Lord et al., 1997; Weston, 2000; Ruhlen et al., 2003). In addition, no research has examined the ecology or conservation of the Malaysian plover, even though they are near-threatened and there has been substantial growth in beach development throughout their range. The Malaysian plover is a sedentary shorebird that breeds on beaches in Southeast Asia (IUCN, 2006). Biparental incubation begins after the first egg is laid and extends for 25 to 35 days (Yasué, M. unpublished data). In the study area the breeding season extends from early April until August (Summer-Smith, 1981).

Study area

All data were collected on a 40 km stretch of beach in Prachuap Khiri Khan province (120 05′ N 990 56′ E) in the Gulf of Thailand between 25 April and 25 July in 2004 and 2005. This study area was selected because it is one of the only remaining, relatively undisturbed beaches throughout Thailand with a significant population of Malaysian plovers (Round, P. unpublished data). Most of the breeding territories consisted of an extensive mudflat (20 – 400 m exposed at low tide) and a 5 – 40 m wide beach backed by mangroves, *Casuarina* trees, *Acacia* scrubland, coconut plantations or abandoned shrimp ponds. The weather from April to May is hot, humid and sunny (diurnal temperature range 28 – 42 ^{0}C) . Later in the season the weather is cooler (26 – 38 ^{0}C), cloudier and wetter.

1) Nest monitoring

I found nests by searching in areas where pairs were frequently sighted, or by watching birds return to nests. Eggs were floated every one to two weeks to estimate lay date and hatch date (based on 30 day incubation period, (Westerskov, 1950) and also detect embryo mortality. Nests were checked every three to five days to assess nest survival and causes of failure. Checks were conducted more frequently close to hatch date because of the high mortality rates of day-old chicks. Predation was assumed to be the cause of nest failure for nests that disappeared between checks, which showed no sign of trampling, inundation, or burial by sand and were more than five days from the predicted hatch date (Yasué and Dearden, 2006c). During nest checks I also resighted adults so that it was possible to differentiate between desertion and predation as causes of failure.

Close to the hatch date, I visited nests every day and recorded the number of peeping or pipped eggs so that it was possible to predict and visit the nest on hatch day. Consequently it was possible to discriminate between nests that were predated before hatch and successful nests in which the chicks died soon after hatch. Behavioural observations of adults and chicks helped determine whether nests had failed or succeeded. Adults with failed nests roosted or fed in pairs on the mudflat, whereas adults with young chicks conducted conspicuous distractive displays when people approached nesting territories. It was also not difficult to count chicks because chicks did not move more than 200 m away from nesting habitats and broods were restricted to a narrow band of beach habitat. Details on non-predation causes of nest failure and responses of plovers to disturbances are presented in a separate study (Yasué and Dearden, 2006c).

Of the 61 and 86 nesting attempts monitored in 2004 and 2005, I observed 73 nests to measure attendance (proportion of time adults incubated or shaded nests). Observations were conducted from a hide or from a seated position more than 100 - 150 m away from the nest, and lasted for 1 to 2 hours (mean length of observations ± SE = 91.5 ± 4.43 min, total 106 hours). At each nest the start and end times of incubation bouts were recorded for both male and female plovers. In addition, shaded air temperature was recorded at a height of 20 cm at the observer's location and percentage cloud cover was visually estimated every 30 min to 1 hour. At the end of the nest observation, I recorded the shaded air temperature and percentage cloud cover. These final weather measurements were used in the subsequent models. Immediately after recording the weather data, one person then approached the nest by walking directly to the nest at a speed of 50 m/minute. Prior to these tests, I used a timer to ensure that disturbance stimuli were standardised and that there was little variability in approach speed. The person disturbing the nest stopped 1 m from the nest for 5 seconds and then walked back to the hide or viewing location at a speed of 50 m/minute. The timer was started when the disturber began to walk away from the nest and I recorded the time taken for adults to return to the nest (seconds). For all trials, it took between 60 to 130 seconds for the disturber to walk back from the nest to viewing location. At the initial viewing location, I sat down and waited for the bird to return. The birds frequently returned to the nest before the disturber reached initial viewing location. Any replicate disturbance trials were conducted at least 1 week apart on the nest to minimize habituation to standardized disturbance stimuli (Parmelee, 1970; Gochfeld, 1984). It is unlikely that birds responded differently to successive trials due to habituation to my standardized disturbances because birds regularly experienced similar stimuli when local people walked along the mudflat and beaches.

If there was a non-experimental disturbance during disturbance trials, this nest return time was not included in subsequent analysis. If there was a non-experimental disturbance at the end of the predator or disturbance surveys I waited for the plovers to resume incubation for at least ten minutes before invoking a standardised disturbance.

Egg temperature regression model

The egg temperature model was developed by measuring temperature and cloud cover and using a regression analysis to predict temperatures inside quail eggs which have similar pigmentation and size (Independent Samples T-test comparison of quail and Malaysian plover egg dimensions: $n_{\text{Quail}}/n_{\text{MaPl}} = 42/136$, length $t = -1.73$ $P = 0.085$, width $t = -1.80$, $P = 0.082$, mass $t = -1.85$, $P = 0.072$). Although quail eggs were slightly larger (at an α level of 0.10), they were the closest sized eggs available. Three quail eggs were placed inside a recently (within 4 days) disused, Malaysian plover nest cup. First the three eggs were shaded using an elevated cloth plover model that was a similar size and colour to a Malaysian plover for 20 minutes. Then I punctured a small hole in one of the quail egg using a needle and put a 1 mm thick probe from an Omega HHM32 Multimeter Thermocouple into the egg. The sensor was situated near the top surface of the egg, where the embryo is located (Drent, 1975). Then the cloth shading the eggs was removed and the temperature inside the exposed eggs after 1, 2, 3, 5, 10, 15, 20, 25 and 30 minutes was recorded. At the end of the trial, I measured cloud cover and shaded air temperature using the same methods as during the nest watch. Forty-two trials were conducted over 13 days in 6 different nest cups. I used a multiple regression using shaded ambient temperature, cloud cover, time of day and the square of time of day as predictive variables (to account for non-linear effects, (Attrill, 2002). For all subsequent analysis this model was used to estimate egg temperature based on the shaded air temperature, cloud cover and time of day that was measured during nest watches (Appendix 1).

2) Factors affecting nest return times

If I conducted more than one disturbance trial on different days at the same nest, one of the trials was randomly selected for the analysis to avoid pseudoreplication. Thus 73 trials were conducted on 73 different nests. ANCOVA was used to examine the effects of modeled egg temperature, embryonic age, time of day, weeks into the breeding season and attendance prior to the disturbance on return times. In addition it appeared that birds returned to nests slower and spent less time on the nests in the afternoon than the morning, independently of temperature effects. Thus time of day, in two categories (8:00 – 12:59 and 13:00 – 18:00) was also included in the model. A binary variable was used instead of a continuous variable because return times varied more between mornings and afternoons rather than by hour. This was visually assessed by plotting 95 % confidence intervals of the effect of time of day (hour, 8:00 – 18:00) on nest return times while controlling for other significant variables. I also included interaction terms between modeled egg temperature and age (days since the start of incubation) because of the age-dependent vulnerability in heat stress for an embryo (Dawes, 1979). The percentage of time plovers spent incubating nests was divided into three categories because the data were strongly negatively skewed. The time taken for birds to return to the nest was log-transformed (base-10) to approximate a normal curve. All five variables and the interaction term were entered into the model. I sequentially removed variables that were insignificant and did not improve the fit of the model.

3) Predator and disturbance surveys

I recorded any natural or anthropogenic disturbances that occurred during the 106 hours of nest attendance observations prior to standardised disturbances. In addition to these surveys, I conducted 241 hours of disturbance surveys at 87 nests in the same study area (mean length of observation 80.41 min). For all surveys, I calculated the total amount of time (seconds) in which plovers left the nest due to the presence of people, dogs, livestock, false alarms and predators. False alarms occurred when plovers responded to a species such as an osprey or curlew that posed no apparent predation risk. Birds were considered "disturbed" if they were exhibiting anti-predatory behaviour such as neck out-stretched vigilance posture, flushing onto the mudflat, "rat-running", chasing intruders, calling to distract predators, false brooding or crouching (Gochfeld, 1984). If birds did not exhibit any of these behaviours and simply left the nest, birds were assumed to be switching incubation duties. Usually the bird leaving the nest would run onto the mudflat to feed or cool its body in tidal pools.

4) Relationship between nest return times and hatch success

Part of the variability in return times may be influenced by individual nest or bird characteristics. To examine whether these characteristics affected the return times, each nest was identified by a number (nest I.D.) and repeatability measurements were calculated at nests in which I had conducted replicate samples. Repeatability is the proportion of variability among individuals as compared to within individuals (Lessells and Boag, 1987; Gorman and Nager, 2003). Thus this measure indicated the strength of the effect of individual nest characteristics. In addition, repeatability indicates how well the single nest return times measured in 46 of the nests reflected the typical behaviour for birds at each nest. Low repeatability suggests that nest I.D. accounted for a very small proportion of the variation in nest return times, undermining the validity of any statistical relationship that may be identified between return times and hatch success. Of the 28 nests with replicate measures, there were 2 trials at 21 nests, 4 trials at 3 nests and 4 trials at 4 nests (total 70 trials).

An ANCOVA was conducted on a subset of the 70 trials, by randomly sampling 1 nest out of each set of replicates for the same nest. Based on this analysis only egg temperature from my regression model, had a significant effect ($P = 0.003$) on nest return times, thus clutch age ($P = 0.945$) and time of day ($P = 0.286$), were not included in further analysis for these 28 nests. The variance component for nest I.D. was then calculated using minimum norm quadratic unbiased estimators (Swallow and Searle, 1978; Sokal and Rohlf, 1981). All 70 trials were included in this analysis and the effect of egg temperature (covariate) was statistically controlled. This variance component was divided by the total variance (within and among group variance) to calculate repeatability. Repeatability was also calculated using the sums of squares method as outlined by Lessells and Boag (1987).

Finally I used binary logistic regression to assess whether return times influenced hatch success. Lay date (Sandercock et al., 1999) and clutch age (Martin et al., 2000) were statistically controlled because both of these factors may influence hatch success in ground nesting shorebirds. The effect of egg temperature was also controlled because in coastal Thailand the fitness consequence of leaving a nest unattended during hot weather is greater than in cool weather. Analyses were run separately for 2004 and 2005 because of the lower hatch success rates in 2005 (Yasué and Dearden, 2006c).

I conducted all data analysis using SPSS version 11.0 (2001). All r^2 values presented throughout are adjusted values. All error bars represent standard errors. A significance level of $\alpha \leq 0.05$ (two tailed) was used for all statistical tests.

Results

1) Nest monitoring

Predation of nests

Strong winds, frequent rains, and hard substrate around nests limited detection and identification of predator footprints. Predation appeared to account for 30 % of nest failure in 2004 (out of 22 failed nests), and 32 % in 2005 (out of 47 failed nests). Of the 22 depredated nests there were only four cases in which partial clutches disappeared. Aside from three nests in which broken or punctured eggs were found, eggs disappeared from one check to the next, and there were no remaining signs of the predator (egg shells or foot prints). This suggests that the predators swallowed the egg whole, or carried the eggs away from the nest. As very few predators were observed during surveys, it is possible that nocturnal predators such as snakes (Stake et al., 2005) may have depredated some of the nests. On one morning, I found the tracks of a large snake near a Malaysian plover nest, with plover tracks weaving back and forth along the snake tracks, indicating that the plover was attempting to lead the snake away from its nest.

Egg temperature regression model

There was no strong multicollinearity in the independent variables that were used to predict quail egg temperature (Pearson's $r < 0.330$ for all bivariate comparisons, Variable Inflation Factor (VIF) ranged from 1.1 -1.2, tolerance ranged from 0.82 – 0.89) (Hair et al., 1998). The resulting regression was significant (all independent variables $P < 0.001$, $r^2 = 0.88$). This modeled egg temperature was used in subsequent analysis (Equation V-1).

Equation V-1 Egg temperature model.

$T_{egg} = -12.86 + 0.906 \times T_{sa} - 0.345 \times C + 3.57 \times H - 0.143 \times H^2$.
Where T_{egg} = Temperature inside egg after 15 min of exposure
T_{sa} = Shaded ambient temperature
C = Percent cloud cover
H = Time of day (hours)

2) Factors affecting nest return times

Plovers responded to humans, dogs and mongoose in the same way. Beach plovers would sneak away from the nest and run onto the mudflat or 20 to 30 m away from the nest along the beach. Then they would approach or circle the disturber, call, feign injury or false brood (Gochfeld, 1984; Montgomerie and Weatherhead, 1988). When the disturber began to walk away, plovers continued to follow the disturber for 30 to 100 m from the nest. Eventually the plovers would run back out to the mudflat directly in front of the nest, and then discreetly and quickly return directly to the nest. Salt flat birds also responded in a similar way to people. If the people were on the beaches adjacent to their nesting territory, salt flat birds would frequently fly out onto the mudflat or beaches to conduct distraction displays. If people walked along the salt flat, then birds tended to display in the salt flat and try to lead the person onto the mudflat or beaches.

When approached by cattle or motor vehicles, plovers tended to either remain on the nest or stay on the nest until the disturber had approached within 5 – 10 m of the nest. Beach plovers would quickly run out to the mudflat directly in front of the nest and then return to the nest and salt flat plovers did not fly to the mudflats, but rather ran 30 – 50 m away from the nest and conducted distraction displays within the salt flats. When ghost crabs (*Ocypode* spp.) approached the nest on beaches, plovers would chase the crab, extend and bat their wings, or feign injury within 1 m of the crab. Finally, when responding to a peregrine falcon or a false alarm caused by another bird, plovers would remain on the nest, crouch and look up (Gochfeld, 1984).

Multicollinearity was not a problem because Pearson's *r*'s values were less than 0.37, VIF factors ranged from 1.1 to 1.6, and tolerance was between 0.69 to 0.96.

Plovers returned to nests faster when modeled egg temperature was higher (**Table V-I**). Modeled egg temperatures ranged from 30 C^0 to 46 C^0. On cool days, birds followed the disturber away from the nest whereas when egg temperature was very high, plovers often did not follow the disturber and instead ran directly back to the nest after the disturber had passed. Plovers took a longer time before resuming incubation if they had older embryos. Embryo age varied from 0 (lay date) to 40 days. Days into the breeding season had no effect on nest return times. Birds with low attendance prior to the disturbance had longer nest return time and birds returned to nests faster in the mornings than in the afternoons (**Table V-I**).

Table V-I Factors affecting nest return times.
Results of ANCOVA showing the factors predicting the return times for Malaysian plovers after a standardised human disturbance ($r^2 = 0.38$, $n = 73$). B = the slope of the line of best fit. The number of days since 1 April ($P = 0.993$), and the interaction between egg temperature and clutch age ($P = 0.368$) were insignificant and so were excluded from the model.

Factor		B	df	F	P
Modeled egg temperature(°C)		-0.04	1	7.07	0.010
Embryo Age (d)		0.009	1	4.47	0.038
Time of day	08:00-12:59	-0.25	1	9.52	0.003
	13:00-18:00	0.000			
Attendance (%)	>90	0.27	2	4.44	0.015
	69-90	0.29			
	<69	0.000			

Although there was no significant interaction term between modeled egg temperature and embryo age when the data were split into even-sized temperature categories and an ANCOVA was used to examine the effects of embryo age on return times, age influenced return times at mid ($P = 0.012$) or low temperatures ($P = 0.045$) but had no effect at very high temperatures ($P = 0.662$).

3) Predator and disturbance surveys

During 347 hours of observations, incubating plovers only spent 70 sec/hour and 48 sec/hour responding to anthropogenic and natural disturbance, respectively. Out of 343 minutes in which birds responded to anthropogenic disturbances (76 events), 68, 25 and 8 % of the disturbance time were caused by people, dogs and livestock, respectively.

Of the 137 minutes (21 events) plovers responded to natural disturbances 46, 40 and 15 % of the time were caused by false alarms, unknown causes or potential predators. During disturbance surveys plovers distracted one mongoose and three ghost crabs away from nests. Outside of these surveys mongoose, ghost crabs and peregrine falcons were also observed disturbing plovers on four, ten and two other occasions, respectively.

4) Relationship between nest return times and hatch success

Individual nest or parental characteristics accounted for a substantial proportion of the variation in return times (variance components for nest I.D.: 3.26 x (10^{-2}), Error 6.08 x (10^{-2}), repeatability = 0.35). Repeatability calculated based on sum of squares (Lessells and Boag 1987) yielded similar results (0.38).

In 2005, individuals that returned to nests faster after standardised disturbances were less likely to hatch chicks when controlling for days into breeding season ($P = 0.647$), age of clutch ($P = 0.696$) and modeled egg temperature ($P = 0.462$, Binary logistic regression overall model, $\chi^2 = 12.37$, *df*

= 4, n = 51, P = 0.015, model coefficients B = 2.34, *Wald* = 5.35, P = 0.021, **Figure V-1**). However, in 2004, nest return time had no effect on hatch success (Overall model, n = 22, $\chi^2_4 = 2.11$, P = 0.715, model coefficient P = 0.192) when the same variables were controlled.

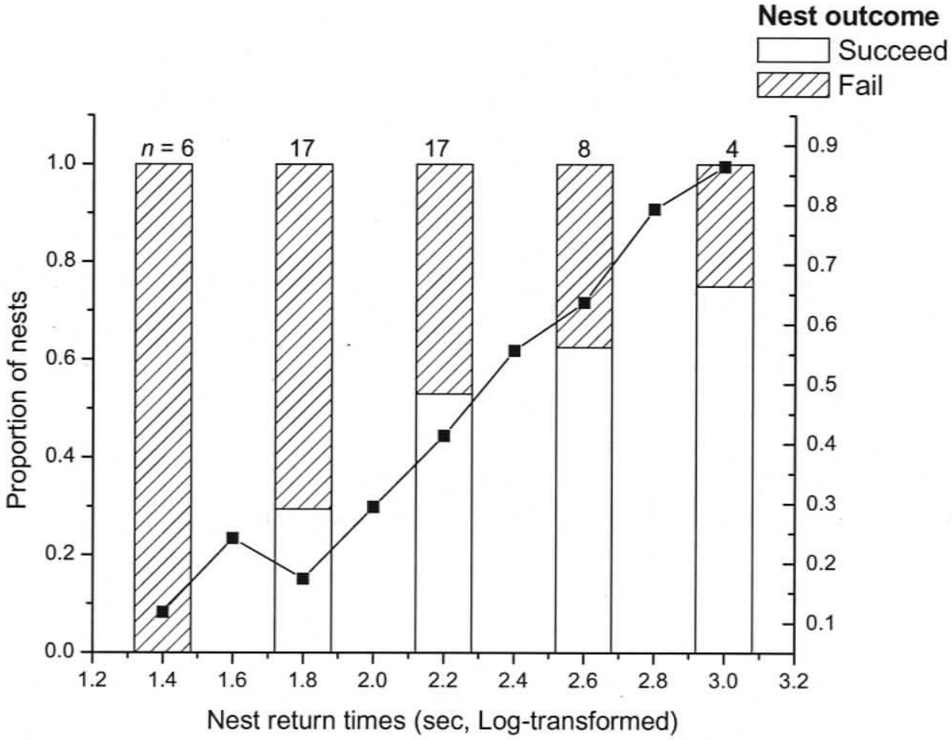


Figure V-1 Nest return times and hatch success.
Results of binary logistic regression showing the effect of nest return times on the probability of hatching at least one egg for 2005. Stacked bars show the proportion of nests that succeeded (unhatched) and failed (hatched) in each nest return time 0.4 sec wide category (location of the bars along x-axis represent medians for categories) and black lines show the predicted probability of success from a model controlling for age of clutch, days into the breeding season and egg temperature.

Discussion

Factors influencing nest return times

On clear days, modeled egg temperatures often exceeded the optimal incubation temperature range for shorebirds [35 - 37 °C according to (Oppenheim and Levin, 1975; Drent, 1975)]. The risk of exposing developing embryos to heat stress appeared to limit the amount of time plovers remained off nests after a disturbance. The effect of heat stress on incubation behaviour has also been observed in other *Charadrius* plovers breeding in hot environments (Wallander, 2003; Amat and Masero, 2004a). On hot days the immediate threat of embryo mortality increases relative to the reduction in predation risk gained by distracting predators and delaying return times. Although temperatures occasionally dropped below optimum incubation temperatures (Drent, 1975; Bennett and Dawson, 1979; Webb, 1987), slight developmental delays due to chilling are unlikely to have a strong effect on breeding success (Norton, 1972) because shorebird embryos are relatively resilient to cooling and temperatures did not drop below 25 °C during my study (Webb, 1987).

Nest return times were longer for older clutches when accounting for the effect of egg temperature. This is because adults may exhibit longer, more intensive distractive displays as the value of the clutch increases (Regelmann and Curio, 1983; Reid and Montgomerie, 1985). These parental investment factors appeared to be more important than the greater sensitivity to heat stress that has been shown in older embryos of other species (Webb, 1987). However, at very high temperatures, birds always returned to nests quickly regardless of embryo age. This suggests that at very high temperatures the risk of heat stress may outweigh parental investment decisions on nest distractive displays.

Days into the breeding season did not influence nest return times. Malaysian plovers are sedentary species with long breeding seasons compared to temperate or arctic species (Sandercock et al., 1999). Consequently in contrast to previous studies (Skutch, 1949; Martin, 1996), the length of the breeding season may not be a significant constraint on productivity. Plovers were observed renesting up to five times and some pairs were able to fledge more than one brood (Yasué and Dearden, 2006a). In addition, the study period did not continue to the end of the breeding season. Thus it is possible that seasonal changes in return times may be detected if trials were conducted in September near the end of the breeding season.

Sources of unexplained variation

Despite carefully selecting and testing several variables, the model accounted for only 38 % of the variability in nest return times. There may be several other factors such as stochastic changes in predator densities, habituation, or nest microclimates that influence both clutch predation risk and thermal environments illustrating the complexity of interpreting the response of wildlife to people. In a similar multivariate study, 11 out of 16 tested variables influenced incubation behaviour and all of these factors together only explained for 57% of the variation behaviour (Regelmann and Curio, 1983).

Predators

Although I attempted to standardize disturbances, the perceived risks were still likely to vary between trials due to the previous experiences of the pair as well as differences in the immediate predator landscape. For example, increased predation risk due to the presence of a mongoose, or habituation due to a large group of people in the vicinity immediately prior to the trial could influence nest return times (Knight and Temple, 1986; Nisbet, 2000).

Compared to other related species, only a small proportion of nests (30 – 32 %) were depredated and few predators were observed (Page et al., 1983; Lauro and Tanagredi, 2002). For these reasons a direct measure of predation risk could not be entered into the model. In other study areas where there is a greater number of visible or detectable predators, the methods used in this study may help to understand the predator landscape in order to improve model predictability (Martin, 1995; Conway and Martin, 2000) and assess the fitness consequences of different nest return times. Future studies focusing on habitat-specific predation risk (Cresswell, 1994a; Rodriguez et al., 2001) as well as seasonal or diurnal changes in predation risk may help to parameterize models.

Nest attendance and return times

Although nest attendance was used to control for individual differences, part of the among-nest variability in return times may not be correlated to nest attendance. For example, a bird in a microsite with high vulnerability to predators may increase bout length to minimize the chance of leading a predator to the nest. In this case, despite greater microsite predation risk, and higher nest return times, overall attendance may not change (Martin and Ghalambor, 1999; Martin et al., 2000). The key factors influencing attendance are the incubation requirements of the nest as well as energetic constraints on the parents ability to incubate (Martin and Ghalambor, 1999). In contrast nest return times are influenced by these above cost-related factors as well as the perception of risk posed by the approaching human (Gochfeld, 1984). Consequently, differences in risk perception could also cause a mismatch between attendance and return times. Risk perception may depend on the habitat or previous experience of the adult. In addition temperature differences between the period when nest attendance was recorded and immediately prior to the standardised disturbance may have caused slight differences in the incubation requirements of the clutch between the two time periods.

Egg temperature model

I used a model to predict egg temperatures based on current weather conditions instead of directly measuring egg temperature. I used this approach because this was the first study conducted on this near-threatened species, and I wanted to reduce the amount of time spent around nests using techniques that could disturb birds in a different way than they experience from other forms of non-researcher disturbance. However, measuring more variables that might influence the thermal environment such as vegetation cover around the nest or global solar radiation measurements may have reduced some of the error in the egg temperature model. Moreover, the temperature of the "shaded" quail eggs may not provide the same level of cooling as adult plovers because shorebirds also cool eggs by belly soaking or panting (Ward, 1990; Brown and Downs, 2003).

Other sources of unexplained variation

Other factors that may account for some of the unexplained variation in nest return times include rainfall, small-scale differences in wind speed around nests (Zerba and Morton, 1983), fluctuations in air temperature and temperature-independent internal incubation rhythms in the parents (Davis et al., 1984) . In addition, it is also possible that variable responses to predators between environments or individuals and flexible anti-predatory behaviours may actually be adaptive and help to reduce predation risk in tropical environments where there is a tremendous diversity of predators that warrant different optimal anti-predation strategies (Schall and Pianka, 1980; Weatherhead and Blouin-Demers, 2004).

Hatching success and return times

In 2005 shorebirds that returned to nests faster were more likely to fail. As shorebirds often respond to broad categories of predators (Gochfeld, 1984), an individual that exhibits strong defensive response to a human may also respond intensely to real predation threats and thus attain higher hatching success (Blancher and Robertson, 1982; Byrkjedal, 1987).

Alternatively, the relationship between hatching success and return times might be a result of differential habitat qualities and territory acquisition abilities (Ens et al., 1992; Byrkjedal et al., 1997). If plovers selected habitats based on microclimate (Walsberg, 1985), the oldest or strongest birds may have secured territories with cooler microclimates and also attained greater success than weaker individuals (Salzman, 1982). Individuals with short return times may also be habituated individuals that are in areas with high non-experimental human disturbance where nests success may be lower. However a concurrent study showed that human disturbance levels in breeding territories did not affect Malaysian plover hatch success in 2005 (Yasué and Dearden, 2006c).

In 2004, nest return times had no significant effect on hatch success. This could be due to different breeding constraints between the years, or lower sample sizes in 2004. Previous studies have demonstrated tremendous inter-year variability in hatch success (Page et al., 1983; Wallander and Andersson, 2003). Factors such as prey availability, weather, changes in the predation environment as well as human disturbance levels may have differed between the two years. Thus long-term studies focusing on habitat or age specific breeding success (Grover and Knopf, 1982; Page et al., 1983) as well as annual variability in nest vulnerability to predation, human disturbance, thermal stress or tidal inundation may help to improve interpretation on the relationship between hatch success and nest return times.

Conservation implications

This study suggests that longer nest return times do not necessarily indicate greater potential fitness impacts (Stillman and Goss-Custard, 2002; Beale and Monaghan, 2004a). If heat stress on eggs was the only factor affecting nest return times and survival, then nests with greater returns times should have had lower hatch success. However, due to the multitude of factors influencing hatch success and parental behaviour, nests with greater return times actually had higher hatch success. Measurements of only nest return times may be an appropriate approach to assess fitness costs of human disturbance in hot environments where heat stress is the dominant cause of nest failure.

Here I demonstrated the value of measuring environmental, ecological and physiological variables that constrain breeding birds, to better interpret a shorebird's response to human disturbance. Egg temperature, embryo age, attendance and time of day should be measured or controlled in future breeding shorebird disturbance studies. These variables may influence both the responses of birds to disturbances as well as the fitness consequences of disturbance (Peters and Otis, 2004). As heat stress appeared to be a key factor influencing nest return times, conservation managers should attempt to reduce human disturbance during the hottest periods of the day when behavioural responses appear to be the mildest. Although birds will usually return to nests quickly during these times, they may not do so if the perceived threat is large enough (eg. a large group of people 2 m from the nest). In my study area, modeled egg temperatures reached lethal levels after only a few minutes of sun exposure. In these cases even short periods of disturbance could impact productivity during hot weather.

Very little is known about shorebird breeding ecology or impacts of disturbance in the tropics (Thomas et al., 2003a). As far as I know, this is one of the first detailed studies on the responses of tropical shorebirds to human disturbance. A better understanding of the natural constraints as well as the environmental conditions or life history traits influencing the vulnerability of wildlife to human disturbance in the tropics could help researchers identify populations or individuals sensitive to disturbance (Weitzman, 1998).

In general, tropical birds may be more sensitive to human disturbance due to the sensitivity of avian embryos to heat stress (Yom-Tov et al., 1978; Morton and Pereyra, 1985). Moreover, currently, almost half of the red-listed shorebirds breed in tropical habitats. Many of these species such as the Javan plover (*Charadrius javanicus*), or Diademed sandpiper-plover (*Phegornis mitchellii*) are thought to be affected by human disturbance (IUCN, 2006). Tropical shorebirds may be more vulnerable to human disturbance compared to arctic species because of the high human densities on tropical beaches (World Resources Institute, 2004). Although human disturbance is also a pressing issue in temperate environments, in most temperate regions there are now stringent visitor regulations, sign-posted exclosures and well-managed protected areas that reduce the impacts of human disturbance (Mayer and Ryan, 1991; Koenen et al., 1996b; Lord et al., 2001; Weston, 2003). In contrast, there are very few examples of these types of conservation strategies in Southeast Asia or in tropical beaches in general.

VI. Are salt flats suitable supplementary nesting habitats for Malaysian plovers *Charadrius peronii* threatened by beach habitat loss in Thailand?

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Abstract

Resort development and coastal beach erosion have lead to declines in beach breeding habitat for the near-threatened Malaysian plover (*Charadrius peronii*) in the Gulf of Thailand. Semi-natural salt flats may provide supplementary nesting areas. I compared the environmental conditions, incubation behaviour and nesting success of plovers breeding on sandy beaches and salt flats in Thailand. In total I monitored 21 and 9 nesting attempts in 2004 (beaches and salt flats, respectively) and 26 and 22 nesting attempts in 2005. Despite higher air temperatures in the salt flats ($P < 0.0001$), I detected no significant differences in nest attendance ($P = 0.542$ and $P = 0.885$ for 2004 and 2005, respectively), number of incubator changes between parents ($P = 0.776$ and $P = 0.823$) and number of parental nest departures ($P = 0.087$ and $P = 0.712$) during 120 incubation observations on 55 nests. There was also no difference in hatch success between beaches in 2004 (Beach = 0.65, Salt flat = 0.55, $P = 0.692$, $n = 26$) and 2005 (Beach = 0.46, Salt flat = 0.35, $P = 0.539$, $n = 41$). These results suggest that salt flats may provide nesting habitat for Malaysian plovers and could help enhance overall hatch success rates by reducing nesting densities on beaches. Although there are few remaining intact salt flats in coastal Thailand there are currently vast areas of abandoned tiger prawn aquaculture ponds that could be rehabilitated into salt flats at relatively low cost. Given the large area of disused aquaculture ponds throughout Thailand and Southeast Asia and the substantial human pressure on coastal habitats, there could be

considerable conservation benefits to the restoration of aquaculture ponds.

Introduction

Sandy tropical beaches are important breeding and foraging areas for waterbirds. However these habitats are threatened by resort development, road construction, coastal erosion, sea-level rise and human disturbance (Burger et al., 1997; Brown and McLachlan, 2002; Yasué and Dearden, 2006c). The population impacts of such habitat changes depend on whether there are alternative areas where waterbirds can use and attain similar levels of survivorship and fecundity (Elphick, 2000; Smart and Gill, 2003). Research relating the values of alternate habitats to wildlife, along with the socioeconomic costs with protecting these areas, can help resource managers cost efficiently partition conservation efforts among different types of habitats (Bernstein et al., 1991).

Malaysian plovers are a red-listed species affected by habitat degradation in beach breeding habitats throughout their range in southeast Asia (IUCN, 2006; Yasué and Dearden, 2006c). In Thailand, coastal development and beach erosion has reduced habitat availability in the main breeding habitats in Petchburi and Prachuap Khiri Khan Provinces on the east coast of Thailand (Yasué and Dearden, 2006c). Beach tourism has tremendous economic importance in Thailand and at present there is little government support to conserve sandy beach habitat for wildlife. Consequently as the Thai economy continues to improve and domestic tourism expands many more beach habitats will probably be lost to commercial development.

A previous study on Malaysian plovers suggested that pairs in areas of high conspecific nest density had lower hatch success (Yasué and Dearden, 2006c). If Malaysian plover populations are limited by breeding success and habitat availability, seasonal, semi-natural salt flats may provide supplementary nesting areas which could reduce beach nesting densities and buffer the population impacts of habitat loss.

These salt flats are formed by natural tidal inundation as well as anthropogenic dyking or channelisation for aquaculture, mangrove reforestation and the creation of salt evaporation ponds. They are sparsely vegetated with mangrove and halophyte vegetation and because they are only inundated during high level high tides that occur during the winter, they provide supratidal foraging habitat for a range of wintering waterbirds during low and mid tides (Velasquez and Hockey, 1992; Weber and Haig, 1997) and also breeding habitats for species such as Malaysian plovers, black-winged stilts *Himantopus himantopus*, little terns *Sterna albifrons* and red-wattled lapwings *Vanellus indicus* during the summer when maximum high tides are lower (Round, P. unpublished data).

To date, aside from anecdotal or census information, few studies have examined the breeding ecology of the Malaysian plover and limited research has been conducted on the habitat use of tropical salt flats by shorebirds in general (Gorman and Haig, 2002). In Khao Sam Roi Yod National Park (KSRY), Malaysian plovers nest either on coastal sandy beaches that are immediately next to tidal mudflats, or on salt flats. Salt flats are adjacent to the sandy beaches (i.e. beaches are located between salt flats and mudflats) and both habitats are available throughout the entire breeding season. Consequently KSRY provides an excellent opportunity to assess the relative habitat value of salt flats.

In this study I compared environmental factors that affect behaviour and breeding success in shorebirds. These factors include thermal stress (Brown and Downs, 2003; Amat and Masero, 2004a), predation risk (Brook and Tanacredi, 2002; Amat and Masero, 2004b), flood risk (Round et al., 2004), and human disturbance or trampling (Weston, 2000; Ruhlen et al., 2003). Although foraging quality is another factor influencing habitat selection in shorebirds (Ens et al., 1992), this was not examined in my study because both beach and salt flat adults and chicks fed together on the mudflats in front of the beaches.

Thermal regulation of clutches is a key factor influencing avian breeding success (White and Kinney, 1974). In tropical environments shorebirds must shade eggs to prevent over-heating (Ward, 1990). Air temperatures may be greater on salt flats than beaches because a 5 to 40 m wide vegetated border between the beaches and salt flats prevents cool oceanic breezes from reaching the salt flats. Adults in hot environments may spend more time attending nests because of the greater need to shade eggs (Carey, 1980; Weathers and Sullivan, 1981; Ward, 1990). Also birds may alternate incubation duties more frequently between mates during hot weather to reduce excessive heat stress on adults (Ward, 1990). There may be higher attendance, higher rates of nest abandonment and lower hatch success on salt flats because unattended nests on salt flats may quickly reach lethal temperatures (Dunning and Bowers, 1990; Conway and Martin, 2000; Amat and Masero, 2004b).

The vulnerability of nests to predators may also differ between the two habitats. The extent of vegetation cover and proximity to water can influence predator density and a nest's vulnerability to predators (Page et al., 1985; Burger, 1987; Pampush and Anthony, 1993; Wolff et al., 1999). There may be higher densities of marine predators (eg. crabs) on beaches and higher densities of mangrove predators (eg. snakes and mongoose) on salt flats. On salt flats the dykes or Acacia and mangrove bushes surrounding most salt flats may lower visibility and reduce an incubating adult's ability to see approaching predators. Moreover nests on salt flats may also be more vulnerable to predators because the vegetation between salt flats and beaches prevent adults that are feeding on the mudflat from detecting predators approaching the nest. In contrast, due to the open structure of the beach, beach-breeding plovers can simultaneously feed and watch for predators. When predators are detected *Charadrius* plovers conduct distraction displays or attack predators to reduce predation rates (Gochfeld, 1984; Yasué and Dearden, 2006b).

Nests located on narrow strips of sandy beach are vulnerable to tidal inundation during very high level tides or storm surges (Eyler et al., 1999; Round et al., 2004). Salt flat nests are less vulnerable to floods because of the slightly elevated vegetated area between beaches and salt flats. Although the salt flats occasionally flood at very high tides in the winter, during the breeding season they were never inundated by tides at KSRY (Yasué, M. unpublished data).

Anthropogenic disturbance could also differ between habitats. Beaches are likely to be favoured transportation routes for people, dogs and cattle because they are more accessible, cooler and less vegetated than saltflats. As a result, beach nesting plovers may spend more time responding to anthropogenic disturbances and suffer greater clutch mortality due to direct trampling (Melvin et al., 1994; Ruhlen et al., 2003).

In this study I compared environmental conditions as well as the behaviour and breeding success of Malaysian plover in sandy beaches and salt flats to evaluate whether salt flats could provide suitable supplementary nesting habitats and help to reduce the population impacts of beach habitat loss.

Methods

Study area

All data were collected within a 5 km stretch of beaches in Khao Sam Roi Yod National Park (990 58′ N 120 06′ E) in Prachuap Khiri Khan Province from 25 April to 25 July in 2004 and 2005. Both beach and salt flat plovers defended 100 – 300 m long linear territories that consisted of a mudflat (20 – 400 m exposed at low tide) as well as a 4 – 80 m wide beach section or salt flat nesting area (Figure VI-1). Both beach and salt flat-nesting pairs fed on the mudflats and hid chicks in the vegetated area next to the beach or on salt flats when there were disturbances on the beach. The vegetated area between beaches and salt flats had short shrubby dune vegetation, mangroves, Acacia bushes or Casuarina trees. Vegetation covered 1 – 30% of the land surface on the salt marsh and the size of individual salt flats (as demarcated by dykes and vegetation) ranged from 2000 m² to 350, 000 m². In contrast to the porous sandy beaches, the substrate on salt flats was hard consolidated mud with a surface layer of evaporated salt.

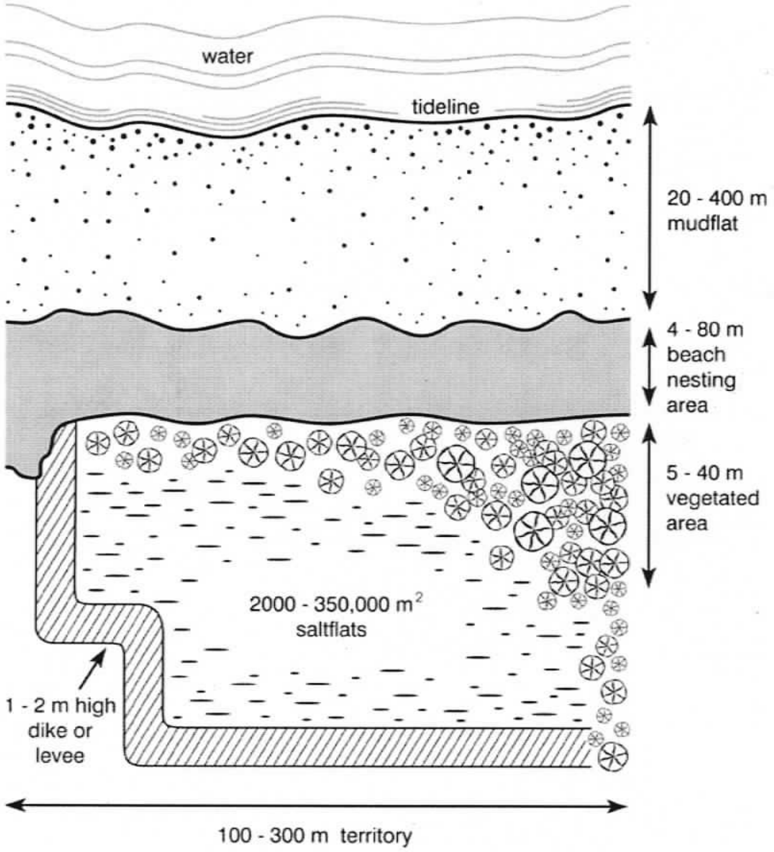

Figure VI-1 Diagram of salt flat and beach nesting habitats.

1) Nest monitoring

I found nests by searching in areas where pairs were frequently observed or by watching birds return to nests. I also floated eggs in water and measured the diameter of eggs above the surface of water in order to detect embryo mortality, estimate lay date and hatch date based on a 30 day incubation period (Westerkov, 1950; Powell, 2001; Yasué and Dearden, 2006a) [see Appendix 2]. I checked the nests every three to five days to determine nest survival or cause of failure. Checks were conducted more frequently close to hatch date because of the high mortality rates of very young chicks. If any clutches less than 25 days old disappeared between checks and there was no sign of inundation (destroyed nest structure, tidal debris at nest) or trampling (crushed nest structure and eggs, tracks of vehicles and footprints) I assumed that eggs were depredated. This was a reasonable assumption because at my study area local people did not collect eggs for consumption. During nest checks I resighted adults to ensure that they were still present and to discriminate between desertion and predation as cause of failure (Yasué and Dearden, 2006c). Detailed observations of adults and chicks helped us to determine whether nests had failed or succeeded. Adults with failed nests roosted or fed in pairs on the mudflat, whereas adults with young chicks conducted conspicuous distractive displays when I approached the nest site. I captured and individually colour banded chicks within two weeks of hatch and returned to the nesting territories weekly to assess chick survival up to 30 days. Assessing fledgling success was not difficult because plovers did not move more than 300 m from the nest sites. Family groups could be identified because at least one of the chicks or adults was individually colour banded. The majority of adults were caught and banded either during the preceding winter, summer or on nests using noose mats or funnel traps (Number of banded adults and chicks: 72 and 94 respectively, (Mehl et al., 2003)).

In total I monitored 21 and 9 nesting attempts in 2004 (beaches and salt flats, respectively) and 26 and 22 nesting attempts in 2005.

2) Nest observations

Thermal stress

I recorded shaded air temperature using a mercury thermometer at a height of 20 cm above the beaches and salt flats several times during the day throughout the course of the study.

I continuously watched incubating plovers using a 15 – 45 X spotting scope or 10 X 50 binoculars for 1 to 2 hours (mean length = [mean + SE] = 81 + 3.2 min) from either a hide or a seated position on the mudflat or elevated position within salt flats located more than 100 m from the plovers. One hundred and twenty incubation watches were conducted on 55 different nests between April and July in 2004 and 2005. No incubation watches were conducted on the same pair on the same day.

Malaysian plovers are biparental incubators and the male and female alternate incubation duties throughout the day. During incubation watches I recorded the time when each of the parents arrived or left the nest.

Attendance was the proportion of time the clutches were incubated by either bird. I also recorded the total number of times the sexes alternated incubation duties and the total number of times either adult left the nest during incubation watches. I standardized values to hourly values.

For nests in which I conducted replicate observations, I calculated mean values for the three incubation behaviour variables and used aggregated values in statistical analysis. However, I considered multiple nests of the same pair as independent. This is because incubation behaviour is influenced by several factors such as nest location and microclimate, weather and time of year that varies between different nesting attempts of the same pair (Carey, 1980; Amat and Masero, 2004b) . The variability in incubation behaviour that results from these factors is likely to be more important than variability that occurs among individual pairs. However, as some pairs nested in both salt flats and beaches in a single year, this may have made my results less likely to detect differences between the habitats.

Vulnerability to predators and flooding

By crouching to the height of a Malaysian plover, I visually estimated the percentage of the circumference around the nest where an incubating plover would be able to detect an approaching predator that is 20 m away. Percentage visibility from nests affects both clutch survival, as well as the predation risk on adults incubating clutches (Wiebe and Martin, 1998; Amat and Masero, 2004b). Visibility is important because plovers rely largely on sight to detect and quickly respond to predators (Amat and Masero, 2004b). I also measured the distance between the nest to the nearest contiguous vegetated area (either the start of the vegetation line adjacent to the beach, or the closest vegetated boundary of the salt flats). This is because predators such as raptors can use vegetation cover to approach and ambush shorebirds (Wolff et al., 1999; Dekker and Ydenberg, 2004). I also measured the distance from the nest to the nearest high tide line based on the location of the strandline and the presence of tidal debris on the beach, in order to assess flood risk. For this analysis, if a single pair of plovers nested more than once on the beach or salt flat in a year, I used mean values of the different nesting attempts in each of the two habitats.

Disturbance responses

I quantified anthropogenic (people, dogs, cattle and vehicles) and natural (predators such as raptors, mammals and crabs, false alarms) disturbance responses by recording the type of disturbance stimuli and the length of time adults response during incubation watches. Birds were categorized as disturbed if they were exhibiting anti-predatory behaviour such as neck out-stretched vigilance posture, flushing onto the mudflat, "rat-running", chasing intruders, calling to distract predators, false brooding or crouching (Gochfeld, 1984). The amount of time birds responded to disturbances was standardised to minutes per hour. Occasionally I was not able to detect the stimuli causing the disturbance response of birds. These disturbances were categorized as "natural disturbances" because anthropogenic stimuli such as cars, people or dogs are unlikely to be missed, whereas natural disturbance stimuli such as cryptic predators or false alarms may be much harder to detect. Frequently birds responded to the rapid flights of other shorebirds or to fish-eating raptors such as osprey *Pandion haliaetus*.

The disturbance measure I used in this study was based on the response of the birds, rather than on the frequency of potential disturbance stimuli. Comparing disturbance stimuli was difficult for this study (eg. the number of people or predators that approach the nest per hour) because the ability for plovers to detect predators probably varied between the two habitats. Moreover, I was able to see very few predators during my study and it is unlikely that I would be able to detect predators in a standardised way without relying on cues from the behaviour of the birds.

For nests in which I conducted replicate observations, I calculated mean values for the anthropogenic and natural disturbance rates and used aggregated values for statistical analysis. I did not pool data between different nesting attempts of the same pair because there is likely to be greater variability between nesting attempts due to seasonal changes in predators (DeCandido et al., 2004) or human disturbance rates and weather rather than between individual pairs.

Statistical analysis

I used a paired t-test to compare the temperature between the beach and salt ponds that were taken in the same hour and within 500 m. If multiple measurements were taken in each habitat during an hour I compared mean values.

For all comparisons of habitat characteristics, behaviours and disturbance rates between beach and salt flats I used a Mann-Whitney's Test of Independent Samples because data could not be normalised using standard data transformations. I conducted analysis for the two years separately to reduce pseudoreplication because several pairs nested at my site in both years.

I calculated hatch success based on the daily exposure method (Mayfield, 1961). A nest that hatched at least one chick was considered "successful" in this study. If a single pair laid more than one clutch within a beach or salt flat in a year, I randomly sampled one of these nests for the Mayfield calculations. Consequently, although a total of 37 and 52 nests were monitored in the two years, my Mayfield nest probabilities were based on 26 and 41 nests. I used a two-sided Fisher's Exact Test to compare hatch success between the two habitats (Dow, 1978; Johnson, 1979) because Fisher's Exact Test is more robust to low sample sizes compared to a Chi-squared Test.

All error estimates presented throughout the text are standard errors.

Results

Although temperature was slightly higher at the salt flats, 34.0 ± 0.3 °C, than on the beaches, 32.2 ± 0.3 °C (Paired t-test $t = -8.7$, $n = 71$, $P < 0.0001$), there was no significant difference in the number of parental changes in incubation duties, number of times an adult left the clutch during an incubation observation, nor nest attendance (**Table VI-I**).

Table VI-I Beach and salt flat incubation behaviour.
Results of Mann-Whitney tests comparing incubation behaviour in beach and salt flat breeding habitats. Sample sizes for beaches and salt flats were $n_{BE} = 15$ and $n_{SF} = 8$ for 2004 and $n_{BE} = 27$ and $n_{SF} = 19$ for 2005.

	Year	*z*	*P*	Pooled Mean
Nest Attendance (Proportion)	2004	-0.9	0.391	0.6 ± 0.1
	2005	-0.2	0.885	0.6 ± 0.1
Number of Incubator Changes (hr^{-1})	2004	-0.3	0.776	0.8 ± 0.2
	2005	-0.2	0.823	0.9 ± 0.2
Number of Adult Clutch Departures (hr^{-1})	2004	-1.7	0.087	1.6 ± 0.3
	2005	-0.4	0.712	1.9 ± 0.2

Salt flats were significantly further from the high tide line and from contiguous vegetation than the beach nests. However, there was no significant difference in percent visibility (Table VI-II).

Table VI-II Beach and salt flat predation and flood risk.
Results of Mann-Whitney comparisons of conditions contributing to predation and flood risk in beach and salt flat breeding habitats. $n_{BE} = 17$ and $n_{SF} = 9$ for 2004 and $n_{BE} = 23$ and $n_{SF} = 14$ for 2005. Significant results are bolded.

		Beach	Salt Flat	*z*	*P*
Visibility (%)	2004	52.8 + 3.5		-1.0	0.312
	2005	50.3 + 3.2		-0.6	0.588
Distance to	2004	6.9 + 1.1	13.3 + 2.8	-2.0	**0.045**
Vegetation (m)	2005	9.8 + 4.5	18.6 + 7.2	-2.1	**0.036**
Distance to tide	2004	6.7 + 0.9	32.2 + 9.5	-2.6	**0.008**
line (m)	2005	10.2 + 1.6	37.5 + 3.8	-4.7	**< 0.001**

Anthropogenic and natural disturbance rates were generally very low for both habitat types (Pooled anthropogenic and natural disturbance rates 2004: Beach 3.6 ± 0.8 min hr^{-1} Salt flat 2.2 ± 0.3 min hr^{-1}; 2005 Beach 0.85 ± 0.3 min hr^{-1} Salt flat 0.33 ± 0.3 min hr^{-1}). Anthropogenic disturbance rates were higher during incubation watches on beach nests in 2005 ($z = -2.4$, $P = 0.019$, $n_{BE} = 33$, $n_{SF} = 22$, Beach 0.7 ± 0.3 min hr^{-1}, Salf flat 0.3 ± 0.3 min hr^{-1}) but not in 2004 ($z = -0.35$, $P = 0.750$, $n_{BE} = 20$, $n_{SF} = 10$, Pooled mean = 2.0 ± 0.62 min hr^{-1}). The main sources of anthropogenic disturbances were local fishers, cattle or motor vehicles. I only detected two disturbance responses caused by natural predators on salt flats. Consequently, I did not conduct tests to compare natural disturbance rates between the two habitat types.

Breeding success and renesting behaviour

There was no significant difference in hatching success between the two habitats in 2004 (Fisher's Exact Test, $n = 26$, $P = 0.692$) or 2005 ($n = 41$, $P = 0.539$, Table VI-III). I could not use a Pearson's chi-squared test to assess whether the number of nests that failed due to flooding, desertion, or predation varied between the two habitats due to low cell counts in contingency tables (Dow, 1978) and so I present a descriptive graph of the causes of nest failure in the two years.

Nine nests failed on the beaches due to tidal inundation (Figure VI-2). In contrast only one of the salt flat nests failed because of flooding during a period of intense rainfall in May of 2004 (90 mm in two days, and the greatest rainfall in a 24 hour period between May and August since at least 1994 according to a national meteorological weather station in Hua Hin city, 99^{0} 57′ N 12^{0} 36′ E). Water could not penetrate through the surface layer of the salt flat and pooled on the salt flat. This type of flooding is unlikely to be significant source or mortality in most years because of the rarity of such intense rainfall during the breeding season. No other salt flat nests were flooded, despite moderate rain in 2004 and 2005 (15 – 20 mm in one day). In general, flood risk should be higher on the beach than the salt flats because beaches are always closer to the tidal edge and they were in between salt flats and the tidal edge. If the tide inundated the salt flat, then in the study area, the beach habitat would also be inundated.

Table VI-III Beach and salt flat nest success.
Mayfield nest success calculated based on nest daily survival rates. Total nests found and failed include multiple nests from the same pair in the same habitat (columns 1 and 2 from left). Nest success was calculated based on nest survival by sampling one of the nests of the same pair in each habitat (columns 3 and 4). Nests succeeded if they hatched at least one chick.

	Total Nests Found	Total Nests Failed	Nests Found	Nests Failed	Mayfield Nest-days	Nest Success
2004						
Beach	26	9	17	5	357	0.65 ± 0.13
Saltflat	11	5	9	4	207	0.55 ± 0.17
2005						
Beach	31	14	24	10	407	0.46 ± 0.11
Salfflat	21	12	17	10	298	0.35 ± 0.12

For most of the suspected depredated nests, entire clutches disappeared between checks and I was unable to identify the predator(Yasué and Dearden, 2006c). I saw small Indian mongoose *Herpestes javanicus* on three occasions (twice on beaches and once on salt flats) in the study area and terns and Malaysian plovers exhibited intense anti-predation responses. On six occasions I observed *Ocypode* ghost crabs apparently attempt to predate clutches on beaches. Adult plovers responded by attacking and chasing crabs. Corvids, gulls or other known diurnal avian *Charadrius* plover nest predators (Mayer and Ryan, 1991; Lauro and Tanagredi, 2002) were never observed searching for nests during the course of my study.

There were c. 100 pairs of little terns *Sterna albifrons* sharing the salt flat with Malaysian plovers in Khao Sam Roi Yod. In 2005 there were three nest checks in which entire clusters of five to twenty little tern and a few Malaysian plover nests (within 1 km of each other), were found to be depredated on the salt flats. Predation rates appeared to be marginally higher on the salt flats in 2005 (**Figure VI-2**).

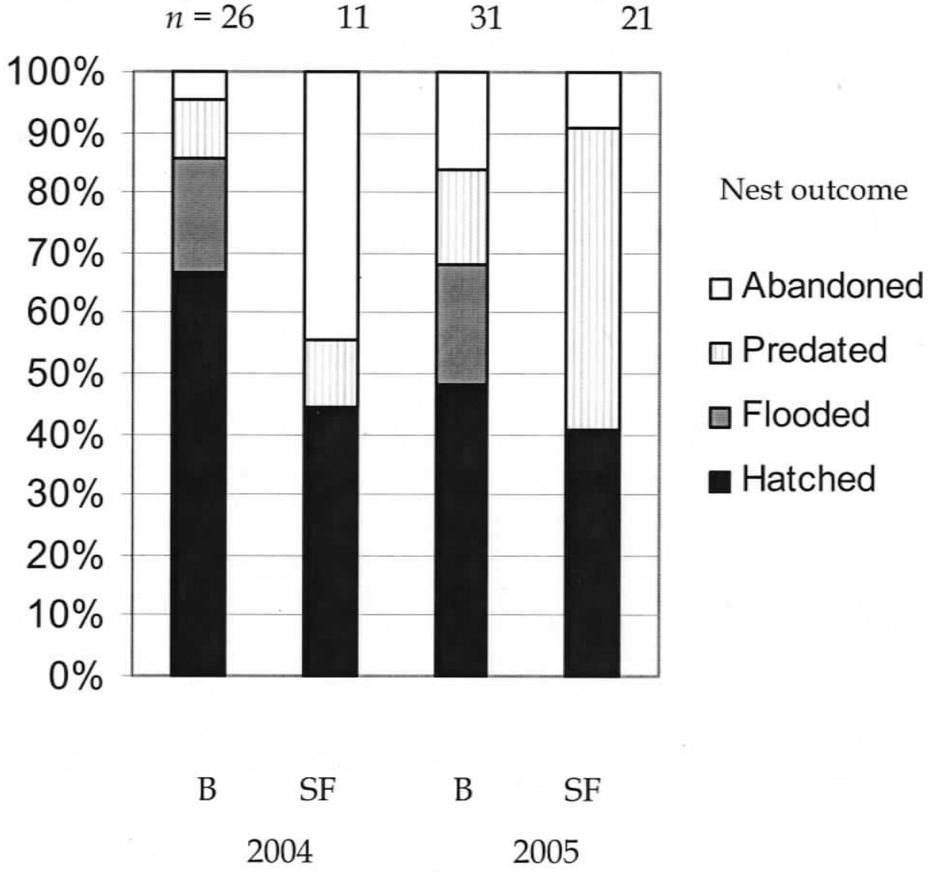

Figure VI-2 Beach and salt flat nest failure.
Cause of nest failure for beach (B) and salt flat (SF) nests in 2004 (left bars) and 2005 (right bars). Sample sizes for each of the bars are denoted above.

After very low success rates at the start of the 2005 breeding season, a significant proportion (58 %) of the birds renested after failed breeding attempts. In 2005, seven of the twelve pairs that nested on salt flats, also nested at least once in the beach habitats. In 2004, three out of four of the pairs that renested, nested in both habitat types in the same year.

I could not statistically compare fledge success rates (the proportion of hatched chicks that fledged) between the two habitats in this study because of insufficient sample size. However, I believe that it was more important to focus on differences in nest success because *both* beach and salt flat-nesting plovers reared chicks on mudflats, beaches and salt flats. In 2004, 81% (*n* = 16) and 80 % (*n* = 5) of nests that hatched chicks, fledged chicks on the beach and salt flats, respectively, while in 2005 10% (*n* = 21) and 17 % (*n* = 6) of the successful nests fledged chicks in the two habitats. It appeared that fledging success rates differed more between years rather than between nesting-habitats.

Discussion

Salt flats as supplementary breeding habitats

The results suggest that salt flats may provide suitable breeding habitat for Malaysian plovers. Contrary to my predictions, there was no evidence indicating that thermal stress or predation risk was greater for birds breeding in the salt flats. Environmental conditions in the salt flats did not differ from beaches sufficiently to impact Malaysian plover breeding behaviour. My results suggest breeding success appeared to vary more between years, rather than between habitats. Thus in some years salt flats may provide nesting areas for Malaysian plovers.

Previous research on *Charadrius* plovers demonstrated substantial annual variability in breeding success due to changes in environmental or ecological conditions (Lauro and Tanagredi, 2002; Wallander and Andersson, 2003). Annual variability in maximum temperatures, beach morphology, maximum water levels and flood-risk, or the presence of a highly effective wide-ranging predator in one of the habitats could influence relative nesting success on sandy beaches and salt flats (Burger, 1987; Koenen et al., 1996a). For these reasons, more studies over several years would be necessary to evaluate the generality of these results.

Based on site visits to beaches throughout both the eastern and western coasts of Thailand and interviews with local bird watchers and Thai academics (Yasué, M. unpublished data), Khao Sam Roi Yod National Park had one of the highest densities of Malaysian plovers in Thailand. This park may be favoured by plovers because it is one of the few areas where semi-natural salt flats still exist next to beaches and have not been replaced by roads, housing or tourism development in coastal Thailand. At KSRY both beaches and salt flats are available and plovers can adjust habitat choice depending on current environmental conditions such as maximum water height or predation risks (Amat and Masero, 2004b). The ability to select different habitat types within a breeding territory may be particularly important for Malaysian plovers because adults appeared to return to the same territory between years (Yasué, M. unpublished data).

In comparison to most other beaches in the Gulf of Thailand, disturbance rates were very low at Khao Sam Roi Yod National Park. There was no evidence of direct trampling on eggs by people in the study area. I did find trampled nests in concurrent studies in other beaches in the Gulf of Thailand (Yasué and Dearden 2006c). Human disturbance on beaches is thought to limit breeding populations in Malaysian plovers (IUCN, 2006; Yasué and Dearden, 2006c)and other related *Charadrius* plovers (Flemming et al., 1988; Ruhlen et al., 2003; Weston and Elgar, 2005a). Disturbance may be a more important difference between these two habitat types in more tourism-oriented beaches and the relative importance of salt flats to Malaysian plover conservation may be greater in other coastal areas of Thailand.

The potential to conserve salt flats and the restoration of aquaculture ponds

Although there are currently few remaining semi-natural salt flats in the Gulf of Thailand, there may be greater potential for conservation of salt flats than beach habitats for two reasons. First, compared to sandy beaches, there is much greater government support for salt flat and wetland conservation in Thailand (Thongchai, 1998; Erftemeijer and Lewis, 1999; Stevenson et al., 1999). The recent enhanced awareness on the economic and ecological value of mangrove forests have lead to salt flat restoration or reforestation initiatives (Macintosh, 1996; Balmford et al., 2002). Second, there may be lower financial costs for governments to conserve salt flats because there are currently vast areas of abandoned and naturalising shrimp (Peneaus monodon) ponds in the Gulf of Thailand (Office of Environmental Policy and Planning (OEPP), 1994; Potaros, 1995; Flaherty and Vandergeest, 1998) and throughout Asia (Sammut and Mohan, 1996; Yap, 1997) that could be naturalised into salt flats (Stevenson et al., 1999). In the 1980s, mangrove forests, natural salt flats and salt evaporation ponds were rapidly converted into high-density industrial tiger prawn aquaculture ponds (Parr et al., 1993). However, water pollution, environmental degradation and disease lead to very high prawn mortality rates and proprietors generally abandoned ponds after three to seven years of use to seek out new areas to construct ponds (Enright, 1995).

The majority of the coast in KSRY is dominated by aquaculture ponds of which 70– 80% are no longer in use (Parr et al., 1993; Enright, 1995; Stevenson et al., 1999). With deep sloping banks preventing any tidal inundation and no vegetation, these disused aquaculture ponds provide none of the wildlife values of the former natural coastal habitats. Park managers or conservation-minded communities could rehabilitate these ponds into semi-natural salt flats to create habitat for plovers and other waterbirds to feed and rear chicks. Removing dykes and allowing partial tidal inundation would help increase invertebrate prey densities and promote natural regeneration of wetland vegetation (Helmers, 1992; Elphick and Oring, 1998). Restoration may have tremendous conservation value because KSRY is the only national park in Thailand with a significant population of Malaysian plovers. In addition to resident species, KSRY has one of the highest densities of migratory shorebirds in the Gulf of Thailand and the salt flats at KSRY provide important supratidal foraging areas for these birds (Yasué, M. unpublished data).

The ability of Malaysian plovers to use abandoned shrimp ponds for both nesting and fledging habitat was demonstrated in one beach 15 km south of KSRY. In July of 2004, after illegal aquaculture operations were closed, these ponds were partially drained and allowed to naturalise. In contrast to other aquaculture ponds in the region abandoned several years ago, these ponds still had permanent pools of water covering 5 to 15 percent of the total area and short shrubby vegetation. In 2005 two pairs of plovers nested and fledged chicks in these aquaculture ponds. Although adults still fed on the mudflats, chicks fed exclusively within the disused aquaculture ponds around the water pools.

Despite the greater potential for habitat rehabilitation of aquaculture ponds, the availability of these abandoned aquaculture ponds still depends precariously on the lack of alternative lucrative land uses. There were several new resorts built near aquaculture ponds in 2005 within Prachuap Khiri Khan and Petchburi Provinces. Without effective protection and active habitat rehabilitation, it is likely that these disused aquaculture ponds will be quickly converted to houses, resorts or roads and lost as potential habitats for birds (Kontogeorgopoulos, 2004). Furthermore, protected area managers have become accustomed to viewing abandoned ponds purely as an environmental problem rather than as a potential area for biodiversity conservation. This research suggests that ponds also offer a considerable opportunity to help augment breeding habitat for certain species if active management measures are taken to assist this process. Given the area covered by abandoned ponds in Southeast Asia and other areas of the tropics, the cumulative effects of rehabilitation on conservation could be substantial.

In this study I could only conduct a statistical comparison of hatch success between the two sites. At present, even pairs that nested on salt flats tended to rear chicks on the beaches. This is probably related to the proximity of the beaches to high quality feeding areas on the mudflats. It is thus possible that beach habitats will still need to be protected to provide chick-rearing habitat. Chicks sometimes fed on salt flats and other *Charadrius* plovers are known to feed in similar salt flat (Koenen et al., 1996a). Similarly to the restoration of aquaculture ponds, habitat management on these salt flats and the removal of some of the historic irrigation channels that have been created for aquaculture or salt production ponds may improve chick-rearing habitat quality in these areas. More research is required to evaluate whether plovers could fledge chicks on only salt flats.

At my site, it appeared that density-dependent reduction in breeding success occurred during the nesting stage (Yasué and Dearden, 2006c) and it is possible that adults moved chicks onto the beaches because they are more able to tolerate higher densities when rearing chicks than saltflats. In addition, as many of the clutches failed at the nest stage, the overall plover densities in beach areas during chick-rearing with both beach and salt flat plovers are still lower because many breeding attempts fail at the nesting stage. Additional studies on the importance of density dependent processes (Dolman and Sutherland, 1995) in the nesting and chick-rearing stages are necessary to evaluate the importance of salt flats to buffer the population impacts of beach habitat loss.

SUMMARY AND CONCLUSION

In my dissertation, I examined the impacts of anthropogenic habitat change on a near-threatened species nesting on sandy tropical beaches. These habitats are understudied and affected by tremendous development pressure. My study is the first to examine the breeding ecology of the Malaysian plover and one of the few studies conducted on breeding shorebirds in Southeast Asia. By conducting research on a tropical plover, this research also contributes to understanding ecological and evolutionary models of avian breeding strategies across a greater range of environmental conditions.

This chapter summarises and synthesises the main findings of the study, whether I was able to meet stated goals and objectives, discusses limitations of the study, and suggests future avenues for research.

Key findings

a) Objective 1: To understand and quantify impacts of beach development

Even within my relatively remote study area, Malaysian plovers appeared to be affected by anthropogenic habitat change. In particular, narrowing of beaches, changes in vegetation cover behind beaches, and increased human disturbance rates lead to lower habitat availability and breeding success in the Malaysian plover. Several of the coastal development projects in the study area occurred within the last few years. As shorebirds are relatively long-lived and have limited clutch sizes (Maclean, 1972), the impacts of these habitat changes may not yet have caused detectable reductions in population sizes (Piersma and Baker, 2000). However it is likely that reductions in habitat availability will eventually affect plover populations because my results suggest a density-dependent decline in breeding success (Goss-Custard et al., 1995).

In addition, the high site fidelity between and within years suggests that there could be a time lag between reductions in habitat quality to lowered numbers of breeding pairs at a particular site. When new construction projects occurred part-way through the breeding season, birds repeatedly renested in the same place even if nests were repeatedly crushed. If plover populations are limited by habitat availability, then they may still try to nest in marginal habitats where they may have low chances of breeding success.

Similarly to previous research, Malaysian plover responses to direct short-term human disturbances depended on a trade-off between the cost (of leaving nests unattended) and the benefits of the response (distraction displays) (Beale and Monaghan, 2004b; Yasué, 2006a). Since animals make such behavioural decisions to maximise fitness, my research contributed to a better understanding of this trade-off and may help managers understand how and when measurements of behavioural responses could be used as proximate measures of potential impacts on wildlife populations.

b) Objective 2: To identify possible differences in vulnerability to anthropogenic change between holarctic and tropical shorebirds

Adult plovers returned to nests faster when exposed clutches were vulnerable to heat stress. Compared to temperate or Arctic shorebirds, tropical shorebirds may be more susceptible to reduced embryonic survival due to human disturbance because embryos are more sensitive to overheating than chilling.

Although some nests failed due to anthropogenic habitat change, Malaysian plovers in the study area generally had high breeding success compared to studies on other *Charadrius* plovers (Koenen et al., 1996b; Lauro and Tanacredi, 2002; Wallander and Andersson, 2003). The long and stable breeding season and productive environments, as well as the low apparent predation rates in the study area, allowed Malaysian plovers to nest several times in the breeding season and sometimes even fledge more than one clutch in a season. Compared to other *Charadrius* plovers, renesting multiple times in a year may have low costs to body condition and future breeding success for Malaysian plovers because they do not migrate, spend only a low proportion of the time incubating nests and appear not to be energetically stressed during the breeding season. Due to these factors Malaysian plover productivity appeared to be less constrained by time and energy than space compared to holarctic shorebirds. Consequently simple changes in land management or the creation of protected areas may be particularly effective in enhancing annual productivity and enhancing populations.

Management Recommendations

If Malaysian plover productivity is constrained more by space than time, restrictions on human access and coastal development in some of the higher quality habitats could help plovers in these areas attain very high annual productivity and increase regional population size. Of the study areas examined in this study, restrictions on development in Khao Sam Roi Yod National Park may be most valuable for conservation because the salt flats at this site provide supplementary foraging, roosting and nesting habitat during both the wintering and breeding season. Moreover, KSRY is also an important wintering area for Malaysian plovers and other shorebirds due to the extensive mudflats with high prey availability (Parr et al., 1993; Enright, 1995).

Visitor access could be restricted along main breeding areas during the hottest months or hours of the day when human disturbance may have the greatest effect on nest success. At several of the study sites, there is substantial motor vehicle traffic along the beach, mainly for local fishers to access boats or shellfish digging areas on the mudflat. Vehicle traffic may have less of an impact on breeding success, compared to walkers or cattle herders, because it is faster, tends to disturb pairs over a short time and is restricted mainly to the harder, wetter mudflat area where birds do not nest. However, previous studies have demonstrated that plover chicks can be crushed by off- road vehicles (Melvin et al., 1994), and this is also a possibility for Malaysian plovers because chicks run back and forth between beaches and mudflats. Once adult plovers detect approaching vehicles, they will quickly lead chicks into the vegetated areas behind the beach. Speed limits on beaches during chick fledging periods may help to reduce the risk of chick trampling by vehicles.

Flood risk appears to limit the amount of available habitat and even the length of the breeding season. Thus in regions that are particularly important for plover, habitats beach heights could be artificially increased to create more suitable habitat (Ziewitz et al., 1992; Round et al., 2004). Although erosion mitigation structures help to maintain beach widths, the creation of seawalls or dikes that run immediately adjacent and parallel to beaches create barriers for chicks, which can not fly and need to quickly access both the vegetated habitat behind the beach to hide, as well as the feeding habitat on the mudflat. Instead, groynes (running perpendicular to beaches) or breakwaters that that are parallel, but separated from the beach by a body of water from the beach should be used. At a more regional scale, adequate environmental impact assessments and more stringent regulations on the construction of roads, houses or jetties at beaches, which promote beach erosion, may help to reduce beach erosion and enhance habitat availability.

When assessing impacts of development projects, time lags between the development project and presence of breeding plovers should be considered because of the high site-fidelity of Malaysian plovers between and within seasons. Even when habitats were altered significantly through the course of the breeding season and Malaysian plovers repeatedly lost clutches, adults did not move to other sites.

Finally, habitat availability may be enhanced by retaining native mangrove or salt marsh vegetation along beaches instead of planting tall *Casuarina* trees and also possibly by restoring disused shrimp aquaculture ponds into salt flats.

Areas of future conservation research on tropical shorebirds

My study suggests that tropical shorebirds could be particularly vulnerable to human disturbance due to the risk of heat stress on clutches. Despite this, almost all disturbance research has focused on temperate species. Of the 20 threatened shorebird species breeding predominately in tropical regions, seven list human disturbance as one of the causes of decline (IUCN, 2006). More research and conservation efforts are required to examine the vulnerability of breeding tropical shorebirds to disturbance.

Although predators play a key role in influencing habitat selection and productivity of shorebirds, in my study I was not able to identify egg and chick predators. Previous studies in Arctic and temperate environments have demonstrated significant reductions in breeding success because of mammalian and avian predators such as corvids (Byrkjedal, 1987; Winton et al., 2000; Larson et al., 2002). The predation environment may be more varied in tropical areas, and include invertebrate predators such as crabs as well as reptiles such as snakes, which are more difficult to detect through direct observations. Research using nest video recorders may help to quantify the impacts of each predator species in different habitats. Understanding the predation environment is important for conservation because enhanced vulnerability to predators may be the proximate cause of anthropogenic habitat-change-related shorebird population declines.

Moreover, due to the hot weather in the tropics, many, marine predators such as Ocypode crabs are more active during the night when desiccation or predation risk is lower. I did not examine nocturnal human disturbance in my study, however villagers often dig for crabs or other marine invertebrates at night. It is possible that human disturbance may flush birds from nests at night and leave clutches vulnerable to nocturnal predators (Bolduc and Guillemette, 2003). In environments where the dominant predators are nocturnal, more research and conservation efforts should be dedicated to understanding the potential impacts of human disturbance at night.

Study limitations

1) Temporal and spatial scale

My research was conducted over a short time period and limited to a relatively small section of beaches. This was the first attempt to examine breeding success in Malaysian plovers, and so it was not possible to assess how representative my results may be compared to other years or locations. There were significant changes to the study area due to coastal development between the two years of data collection. In addition, ecological or environmental variables such as weather, predation pressures and prey availability vary substantially across space or time and could have influenced the results of my study. Significant inter-year differences in productivity and breeding behaviour have been demonstrated in other studies (Wallander and

Andersson, 2003). Longer-term studies are needed to examine the impacts of anthropogenic habitat change and breeding ecology over a larger range of environmental and ecological conditions.

Furthermore, in a two year study it was not possible to measure adult or juvenile survival rates. For long-lived birds breeding in environments with significant inter-year fluctuations in habitat quality, adult survivorship may have a much greater impact on population size than annual productivity (Hitchcock and Gratto-Trevor, 1997; Sandercock et al., 2005). Longer-term research on adult survivorship would permit more accurate population viability analysis so that management efforts could be focused on life history stages that have a disproportionately large effect on population size (Saether and Bakke, 2000; Larson et al., 2002; Dinsmore et al., 2003).

The small study area isolated for my research that probably represents the best remaining Malaysian plover habitat in Thailand. As a result, the anthropogenic impact that I demonstrated is probably much lower in the study area than in other regions of Thailand or perhaps even Southeast Asia. Moreover, results may not be applicable to other regions because there could be unusually high prey densities, or low predator densities at the study area compared to other beaches in Southeast Asia. More multi-factorial human disturbance and habitat loss studies that measure a full range of environmental or ecological factors such as predation rates, prey availability and weather may help to identify conditions in which plovers are vulnerable to adverse impacts of human disturbance and habitat loss.

Finally there is also a need to incorporate the behavioural approaches that I have used in this study, into a regional study to examine larger spatial and temporal scale processes such as juvenile dispersal and temporary or permanent emigration between different beaches (Kotliar and Wiens, 1990; Wiens et al., 1993). Using spatially explicit models with variable rates of productivity, it may be possible to back-cast past changes in populations based on land-use data and prioritise "source" habitats for conservation (Liu et al., 1995; Brawn and Robinson, 1996).

2) Single-species

To design effective land-use management plans, there are obvious limitations to single-species studies. Although several other species such as little terns or sea turtles share beaches and similar habitat requirements to the Malaysian plovers, some of the management recommendations that I have advocated, such as the removal of large *Casuarina* trees, are likely to adversely impact beach forest species. For this reason it is important to undertake multi-species studies and assess the cumulative impacts on a broad range of species. Species should be selected based on the species threat level, within the country or globally, sensitivity of the species to other types of anthropogenic changes, as well as the amount of similar types of habitats in the region or globally (Brooks et al., 2006).

3) Non-migratory

In addition to studying only a single species, I focused my research on a sedentary shorebird, even though the vast majority of shorebird species are migratory. As I discussed in the introduction, there may be greater challenges conserving migratory species. Moreover, there were many more wintering species (24 species, as opposed to 3 breeding shorebirds) in the study area. However, after a preliminary study on wintering migratory birds in 2003, I felt that the potential conservation implications of a study on a sedentary species would be greater because the impacts of development appeared to be much more direct, and easier to quantify, than for migratory shorebirds. In addition, many of these migratory shorebird species, such as the common redshank *Tringa totanus*, Eurasian curlew *Numenius arquata*, or Kentish plover range over several global regions and are well-studied in northern parts of their range, whereas no data existed for the Malaysian plover.

Between 2003 and 2005, I also conducted research on wintering migratory shorebird populations both in Thailand, and in Canada: these data will be presented elsewhere and were not included in my dissertation (Yasué, 2005; Yasué, 2006a). Although human disturbance or habitat loss could affect the amount of available foraging habitat for shorebirds, it is difficult to assess potential impacts on fitness measures, such as breeding success or annual survivorship, in a short-term behavioural study (Gill et al., 2001b). Moreover, the key mechanisms leading to population impacts of anthropogenic habitat change are enhanced predation or starvation risk (Gill et al., 1996; Frid and Dill, 2002; Beale and Monaghan, 2004b). Habitat loss or human disturbance may force birds to feed during periods or in areas where they have lower foraging rates or higher risks from predators. Birds in tropical areas are likely to be less vulnerable to both of these mechanisms (Schneider, 1985). In temperate areas birds have a harder time meeting energy budgets, prey may be more likely to be depleted seasonally and birds may be more vulnerable to avian predators because of the need to maintain higher fat reserves (Cresswell and Whitfield, 1994; Houston, 1998; Cullen and Robertson, 1999). Moreover, in my preliminary research it appeared that there was little evidence for either energetic stress or high predation risk at the study site.

The wider context of conservation

In a two year study, it was possible to assess impacts of coastal development and provide management recommendations for a species in which there has been almost no previous research. There are many characteristics of the Malaysian plover that make it conducive to this kind of research. The birds are visible, site-faithful, sedentary and have very strong, predictable habitat preferences. Moreover, there is a plethora of research in temperate areas on similar species from which I could adapt methodologies. Several of the recommendations that I have made in this study to reduce impacts of anthropogenic change have been implemented in temperate regions and have enhanced breeding populations of *Charadrius* plovers (Mayer and Ryan, 1991; Dowding, 1993; Koenen et al., 1996b). However, it is important to note that this type of ecological research is a small, but necessary, first step in conserving a threatened species.

In stark contrast to the ease in evaluating and recommending biological solutions to increase plover populations, it is much more challenging to address the wider socioeconomic, political and institutional factors that limit the implementation of effective conservation strategies for Malaysian plovers (Beissinger, 1990; Myers, 1998; Sinclair et al., 2000). Malaysian plovers range within a region (Southeast Asia) where environmental conservation and protected areas in nearly all the countries are hindered by insufficient funding, poor enforcement, corruption, poor governance and weak institutions (Dearden, 1995; Vandergeest, 1996; Dearden, 2002; Smith et al., 2003). Moreover, Malaysian plovers also require a type of habitat that is highly valued by people, where development or human-use restrictions could impose significant opportunity costs to Thai people (Ferraro and Kramer, 1997; Balmford and Whitten, 2003). These costs would have negative impacts on important national goals of economic development or the alleviation of rural poverty if local people incur the costs of protection (Schwartzman et al., 2000; Ferraro, 2002).

To offset some of the costs for protection, some conservationists have advocated different forms of economic development, such as ecotourism that couple income generation with wildlife protection (Robinson, 1993; Burger, 2000; Schwartzman et al., 2000; Stoll-Kleemann and O'Riordan, 2002). However this may not be an appropriate strategy for Malaysian plovers because my study suggests that they are intolerant of even low levels of human use. The high sensitivity to even low levels of disturbance or habitat alterations has been illustrated in other beach-breeding *Charadrius* plovers throughout the world (Lord et al., 1997; Leseberg et al., 2000; Ruhlen et al., 2003).

Malaysian plovers also do not possess any of the important characteristics that attract eco-tourists: Unlike Panda bears, hornbills or rhinoceros, they are not unique, critically endangered, charismatic or attractive (Ferraro and Simpson, 2000). They are slightly more rotund, long-legged versions of the globally wide-spread Kentish plover. However due to the large number of shorebirds wintering in the area and the presence of the critically endangered Nordmann's greenshank, there may be some limited potential for birdwatching ecotourism during the non-breeding season. This may create some economic incentives for conservation while still having little adverse impacts on productivity or survival of non-breeding birds in the study area (Gill et al., 2001a). As the region does not have reefs, coralline waters or white sand beaches, it is unlikely that enough people will be attracted to this region so that alternative economic incentives alone would adequately conserve the habitat. Thus there will need to be stricter government regulation on development (especially within the national park) or subsidies to ecotourism operators within the region so that they can compete with much more attractive natural tourist destinations within Thailand and globally.

In the last twenty years, there has been an increase in the amount of money available from developed countries to help offset the biodiversity conservation costs in developing countries (Kramer and Sharma, 1997; Kramer et al., 1997; Balmford et al., 2003). Although several regions of Thailand are within global biodiversity hotspots for conservation (Myers et al., 2000), beach habitats do not have high levels of biodiversity and thus do not receive a significant proportions of this money. The main areas that are prioritised by large conservation initiatives such as Conservation

International or World Wide Fund for Nature as well as supranational sources of funding such as the Global Environmental Facility remain the biodiversity rich, tropical forests (Rodrigues et al., 2004). Although focusing on areas of high biodiversity is probably the most efficient approach to maximise gains from limited conservation funding (Balmford et al., 2003), it is important to note that large tracts of undisturbed and unsettled forests still exist (Gorenflo and Brandon, 2006). This is not the case for beaches.

Finally, in contrast to mangrove forests, which provide erosion control or protection from tsunamis or primary forests that act as water filtration systems or carbon sinks (Kramer and Sharma, 1997; O'Riordan and Stoll-Kleeman, 2002; Farber et al., 2002; Costanza et al., 2002), pristine beach habitats do not have any identified important ecosystem service that could help offset conservation costs. Within Thai protected areas, there has been increased awareness and interest on biodiversity protection in coral reefs, rainforests and now increasingly mangrove forests (McNeely and Dobias, 1991; Sathirathai, 2000; Sudara, 2002). However there is still very little interest to conserve beach habitats, and even many park superintendents view beaches as areas for income generation rather than areas for biodiversity protection. For these reasons, within the larger context for conservation and the limited resources available for global conservation, at present the future for Malaysian plovers seems bleak.

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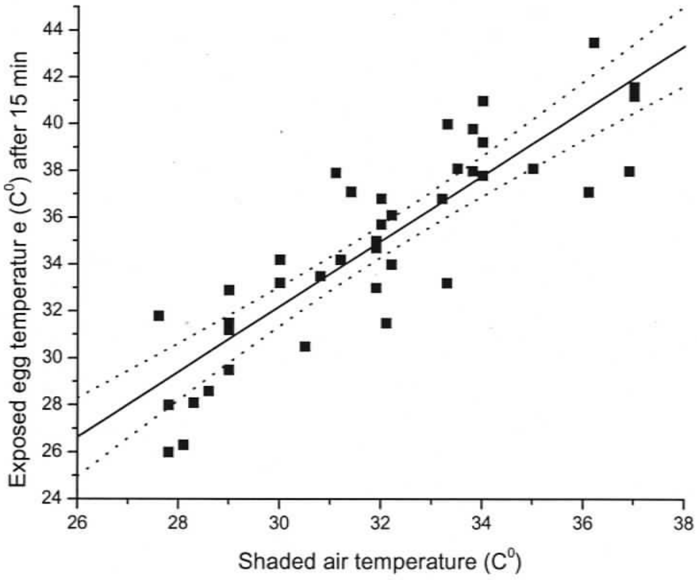
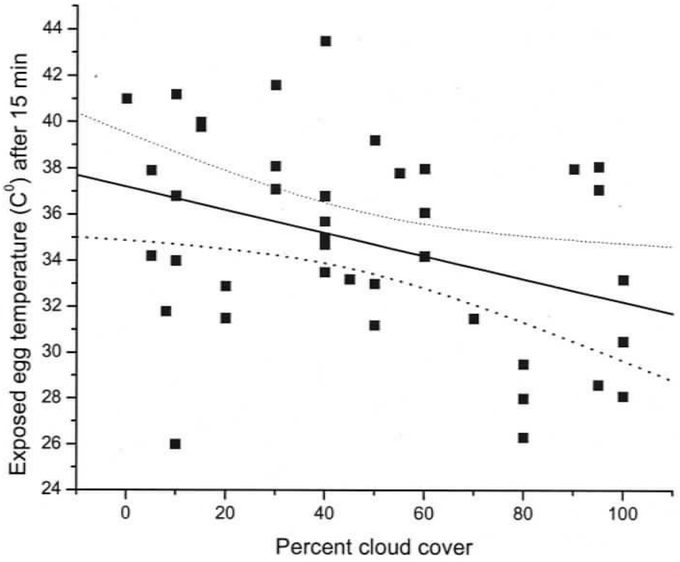
APPENDIX

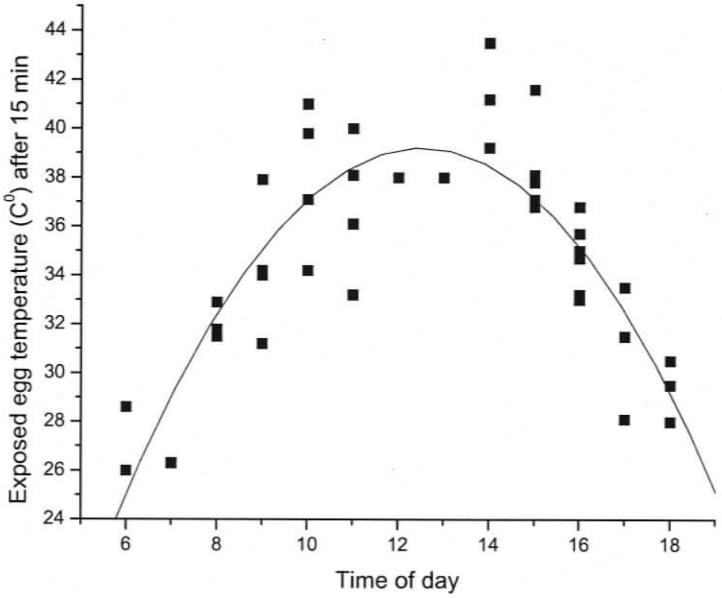
1. Egg temperature model

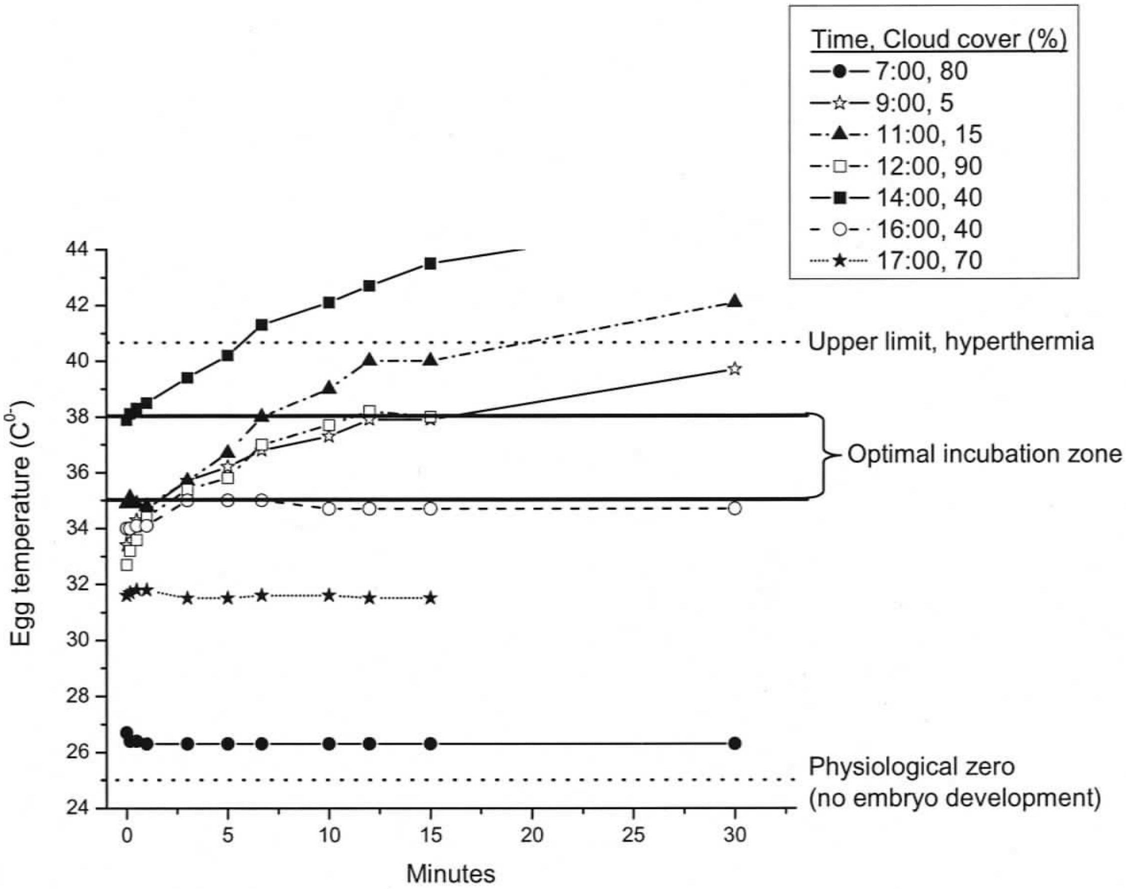
Below are scatter plots showing the relationship between shaded air temperature, cloud cover and time of day which I used to predict the temperature inside an unshaded egg in a nest cup. Dotted lines represent confidence intervals. The last graph shows the increase in temperature with time in an un-shaded quail egg at different levels of cloud cover and time of day.

	df	*F*	*P*
Shaded egg temperature (C^0)	1	37.13	<0.0001
Cloud cover	1	17.46	<0.0001
Hour	1	15.62	0.0004
Hour*Hour	1	15.97	0.0003
Error	36		
Total	41		
Corrected Total	40		




Exposed egg temperature (C^0) after 15 min
24
26
28
30
32
34
36
38
40
42
44
0
20
40
60
80
100
Percent cloud cover

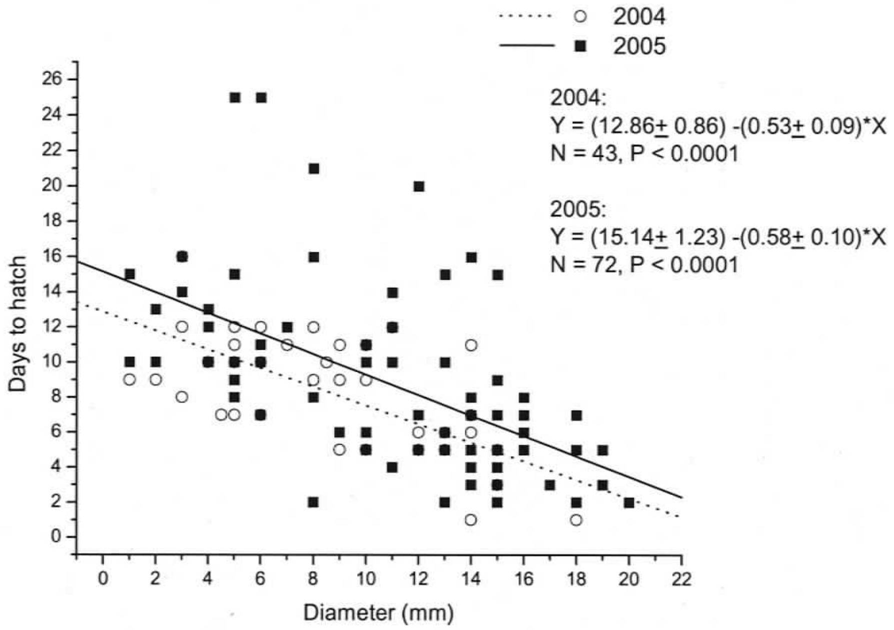

Exposed egg temperature (C^0) after 15 min
24
26
28
30
32
34
36
38
40
42
44
6
8
10
12
14
16
18
Time of day

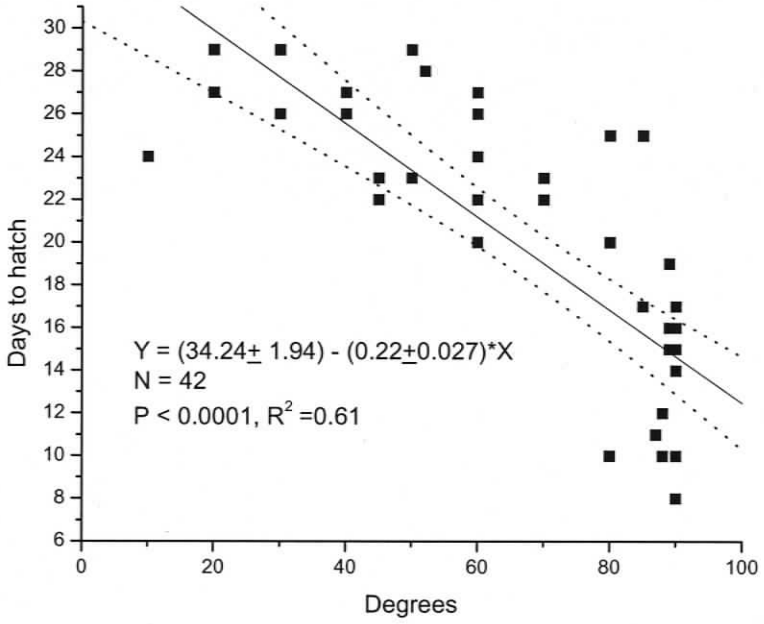


Time, Cloud cover (%)
7:00, 80
9:00, 5
11:00, 15
12:00, 90
14:00, 40
16:00, 40
17:00, 70
Upper limit, hyperthermia
Optimal incubation zone
Physiological zero
(no embryo development)
Egg temperature (C⁰)
Minutes
44
42
40
38
36
34
32
30
28
26
24
0
5
10
15
20
25
30

2. Estimation of days until hatch based on egg floatation method

Eggs were floated in a plastic cup of water and I measured the diameter of the part of the egg that is above the surface of the water. Before eggs begin to float, I measured the angle of the egg floating in water. I used these values to predict the days until clutches would hatch. I could estimate total incubation length based on 21 nests in which I detected the nest between the first and second egg, and also visited the nest on the day when chicks hatched and were still in the nest cup (30.12 ± 0.64, min = 27, max = 39).


2004
2005
2004:
Y = (12.86± 0.86) -(0.53± 0.09)*X
N = 43, P < 0.0001
2005:
Y = (15.14± 1.23) -(0.58± 0.10)*X
N = 72, P < 0.0001
Days to hatch
0
2
4
6
8
10
12
14
16
18
20
22
24
26
Diameter (mm)
0
2
4
6
8
10
12
14
16
18
20
22


Y = (34.24± 1.94) - (0.22±0.027)*X
N = 42
P < 0.0001, R² =0.61
Days to hatch
6
8
10
12
14
16
18
20
22
24
26
28
30
Degrees
0
20
40
60
80
100

3. Adult body dimensions

Table 1. Body dimensions of males and females plovers. Mass was measured using a Pesola spring balance. I also used a wing chord ruler to measure the distance from the tips of the toes of a plover to the tarsus. I only measured each plover one time, when I caught the birds to colour band them either in the winter or breeding season. Sex did not have a significant effect on body mass or wing chord but males had a significantly longer tarsus and tarsus to toes measurements.

			Male			Female		
	t	*P*	Mean	SE	N	Mean	SE	N
Straightened wing chord	1.7	0.094	99.88	0.37	73	99.02	0.35	74
Tarsus to toes (mm)	-4.3	<0.0001	47.75	0.31	65	49.38	0.22	64
Tarsus (mm)	-2.4	0.018	32.18	0.21	28	33.01	0.26	32
Mass (g)	-0.28	0.780	38.40	0.52	68	38.62	0.57	69

Table 2. The mean body mass of plovers that were caught using noose mats in the non-breeding season in 2004 were significantly lighter than individuals that were caught on nests during the breeding season. In this analysis I controlled for body size by including toes to tarsus as a covariate into the model ($F_{1,110} = 31.68, P < 0.0001$).

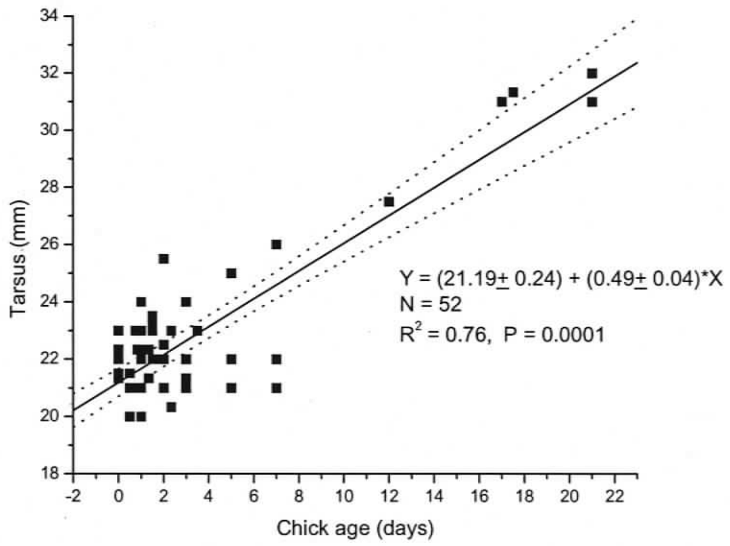
Mass (g)	Male			Female		
	Mean	SE	N	Mean	SE	N
Pre-breeding (Jan - Mar.)	35.23	0.68	21	35.23	0.84	24
Breeding (Mar.-Jul)	40.10	0.66	48	40.13	0.51	44

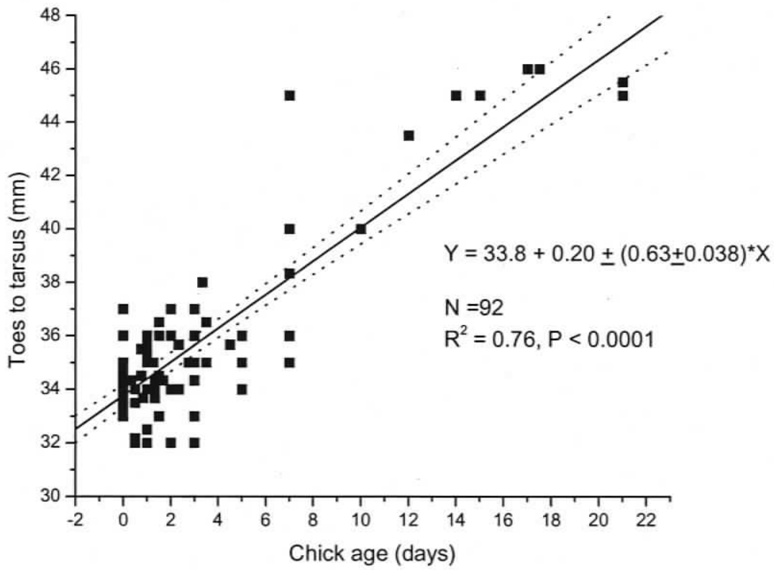
Table 3. When I used an ANCOVA and controlled for body size, the number of weeks since clutches were laid influenced the mass of plovers ($F_{1,106} = 31.6$, $n = 113$, $P < 0.0001$). Sex and year had no effect on body mass and were removed from the model.

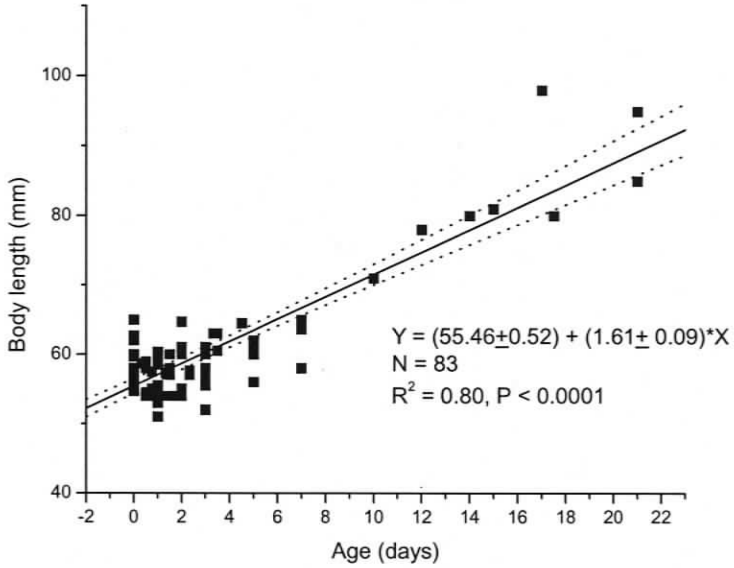
		Mass (g)			Mass/tarsus to toes		
		Mean	SE	N	Mean	SE	N
Pre-breeding		35.23	0.54	45	0.71	0.01	28
Weeks of incubation							
	1	41.88	1.07	21	0.87	0.02	20
	2	39.16	0.47	39	0.81	0.01	34
	3	41.47	1.31	16	0.86	0.03	15
	4	38.87	0.72	15	0.81	0.02	15
Total		38.52	0.39	136	0.80	0.01	112

4. Chick body size

Whenever possible, I measured mass, tarsus, toes to tarsus and body length (tip of bill to rump) when I colour banded chicks. Each chick was only caught once during the two field seasons. Below I show tarsus length, toes to tarsus, body length and body mass as a function of chick age. Almost all chicks were caught within the first 10 days of hatching.






Body length (mm)
100
80
60
40
-2
0
2
4
6
8
10
12
14
16
18
20
22
Age (days)
Y = (55.46±0.52) + (1.61± 0.09)*X
N = 83
R² = 0.80, P < 0.0001

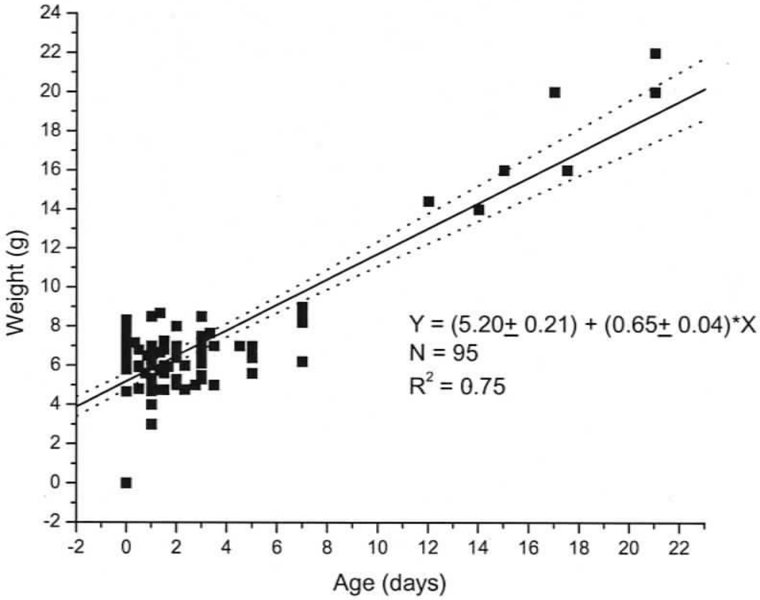
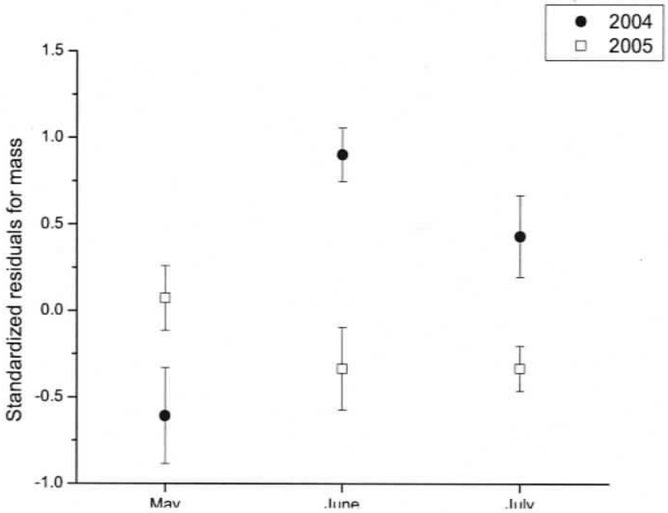
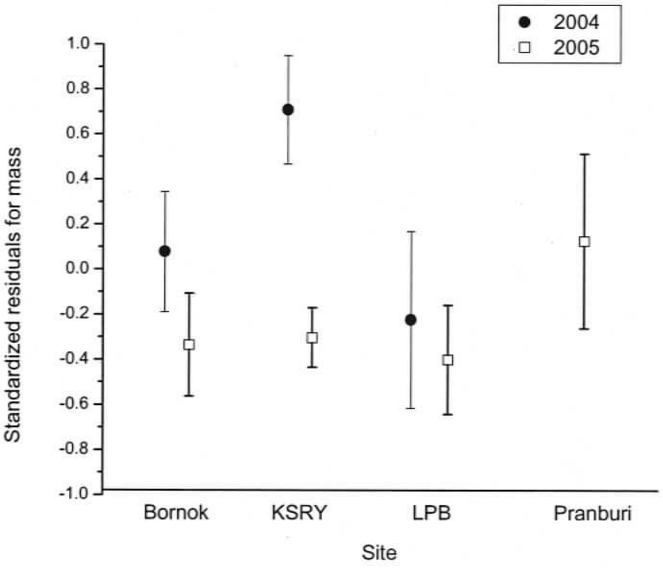

Weight (g)
24
22
20
18
16
14
12
10
8
6
4
2
0
-2
-2
0
2
4
6
8
10
12
14
16
18
20
22
Age (days)
Y = (5.20± 0.21) + (0.65± 0.04)*X
N = 95
R² = 0.75

Table 1. When I used an ANCOVA and controlled for chick age, chick size was influenced by interaction terms between month and year as well as site and year. Error bars below show the effect of month, year and site on the residuals saved from the ANCOVA model.

	df	*F*	*P*
Age (days)	1	355	<0.0001
Month	3	0.14	0.926
Site	3	0.46	0.738
Year	1	0.051	0.836
Month*year	2	15.2	$2.48*(10^{-6})$
Site*year	2	4.57	0.013





5. Factors affecting egg dimensions

I used a Pesola spring balance to measure egg mass. Width and lengths of eggs were measured at the broadest point on the eggs.

Table 1. Dimensions of eggs.

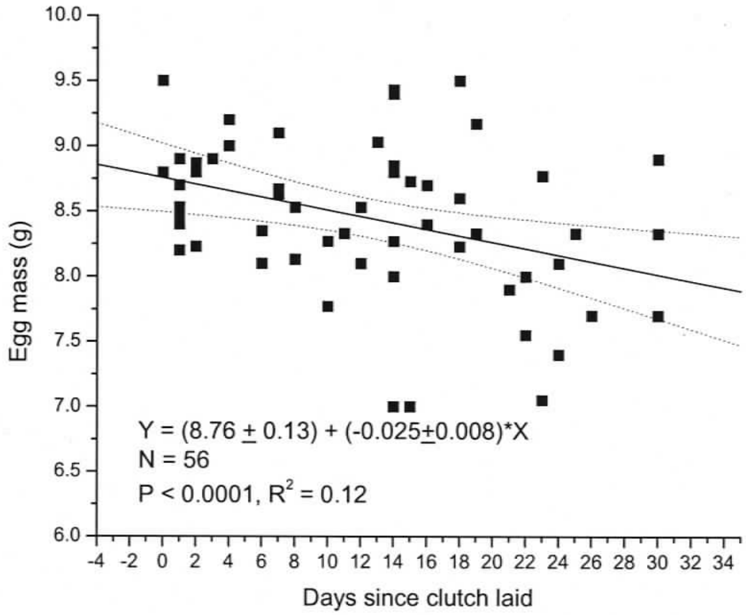
Year	Width (cm)		Length (cm)		Volume (cm^3)		
	mean	SE	mean	SE	mean	SE	N
2004	2.36	0.04	2.91	0.03	8.25	0.24	23
2005	2.35	0.01	3.14	0.02	8.89	0.11	70
Total	2.35	0.01	3.08	0.02	8.73	0.11	

Table 2. Year was the only factor that influenced egg volume ($n = 90$). Year remained significant when all other variables were removed from the model $P = 0.004$). The lay date, clutch size (1, 2, 3, >3), whether it was the first, second or third clutch of the season for a pair, and site had no effect on egg volume.

Volume			
	df	*F*	*P*
Lay date (Days since 01 Apr.)	1	0.17	0.68
Clutch size	3	0.76	0.52
Nest number	2	0.36	0.70
Year	1	6.8	0.011
Site	3	1.9	0.13

Table 3. The number of days since eggs were laid was the only factor that had a significant effect on the mass of eggs. Egg mass was only measured in 2005. Based on the relationship between egg mass and days since clutches were laid, the mean fresh weight of eggs was (8.68 ± 0.07, n = 55).

	df	*F*	*P*
Lay date (Days since 01 Apr.)	1	1.21	0.277
Clutch size	2	2.8	0.073
Nest number	2	0.22	0.800
Site	3	1.15	0.338
Age of embryo (days)	1	9.88	0.003
Error	46		



6. Variance components analysis on the effect of clutch on egg dimensions

I ran variance components analysis to examine the effect of clutch on egg dimensions. Egg width (Repeatability = 0.33, $F_{89,137}$=2.28, $P < 0.0001$), volume (Rep = 0.64, $F_{89,137}$=5.3, $P < 0.0001$)) and fresh weight (Rep = 0.63, $F_{57,95}$=5.4, $P < 0.0001$)) were all significantly affected by clutch I.D, whereas length was not (Rep = 0.08). I statistically controlled for year in these analysis.

7. Egg dimensions of large clutches

Three clutches (Pran5, LPBN53 and Tao7) had more than 3 eggs and there was also one simultaneously double-clutching pairs (Borc51). Below I show the egg dimensions of these large clutches and compare them to the egg dimensions of the rest of the population. Year was the only factor that had a significant effect on egg dimension.

Table 1. Width, length and volume of all eggs in four breeding attempts with more than three eggs.

	Width (cm)	Length (cm)	Volume (cm^3)	Weight (g)
2004				
Borc51: A	2.21	3.00	7.60	
	2.20	3.02	6.92	
	2.10	2.98	6.93	
Borc51: B	22.0	30.1	7.86	
	21.1	31.0	7.60	
2005				
Pran5	2.34	3.27	9.37	7.6
	2.25	3.20	8.48	7.8
	2.35	3.20	9.25	8.1
	2.35	3.10	8.96	8.1
LPBN53	2.35	3.02	8.73	8.2
	2.34	3.21	9.12	7.6
	2.35	3.05	8.81	8.4
	2.45	3.08	9.67	9.0
	2.30	3.21	8.89	6.9
Tao7	2.28	3.34	9.09	9.4
	2.37	3.22	9.47	9.4
	2.44	3.02	9.41	9.5
	2.38	3.42	10.14	8.5
	2.38	3.40	10.08	8.2

Table 2. Comparison of the egg dimensions of these four clutches to other clutches. Borc51 was analysed separately because year had a significant effect

on egg dimensions. Significance values are based on a one sampled t-test and an independent samples t-test.

	Borc51	2004 population	*t*	*df*	*P*
Width (cm)	2.18	2.36	3.98	20	0.001
Length (cm)	3.02	2.91	-3.34	20	0.003
Volume (cm^3)	7.38	8.25	3.44	20	0.003
	Pran5, LPBN53, Tao7	2004 population			
Width (cm)	2.35	2.35	0.30	68	0.768
Length (cm)	3.17	3.14	-1.86	68	0.067
Volume (cm^3)	9.05	8.88	-1.45	68	0.150
Fresh weight (g)	8.45	8.65	2.75	54	0.008

8. Hatch asynchrony

Of the clutches in which I was able to visit the nest on hatch day, 62.3 % (n = 69) of clutches hatched within the same day. There were 26 clutches that hatched asynchronously, 4, 15, 1, and 1 of the clutches hatched over 1, 2, 3, 4 and 6 days. Nests in tropical environments may be more likely to hatch asynchronously because adults must begin shading (or incubating) the clutch immediately after the first egg is laid. Adults began incubating or shading clutches after the first egg was laid.