Sharing the catch; Social and environmental correlates of body condition in threatened Northern Resident killer whales

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Sharing the catch; Social and environmental correlates of body condition in threatened Northern Resident killer whales

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Abstract

Effective conservation and management should consider a species' social dynamics, given that resource scarcity can lead to intragroup conflict. When food is limited, the reallocation of shared resources may incur costs for group members who depend on provisioning or for members that provide shared food. Resident Killer Whales share prey within their stable kin-based groups (matrilines), but little is known about how social group composition might influence allocation of shared prey and associated individual physiological condition. Using drones, we collected aerial images to estimate body condition of Northern Resident Killer Whales over ten years (2014-2023) to evaluate the health of individuals, some across multiple years (n = 175 individuals from 39 matrilines), in a population of approximately 345 whales. Our first objective was to examine the association between individual body condition and the composition of their matrilines, while accounting for salmon availability. Our second objective was to evaluate if mothers with more offspring had lower body condition, and if this relationship depended on their offspring sex. Using two candidate model sets of generalized mixed effect models, we found that social variables influenced body condition. Specifically, males showed declines in body condition as the proportion of juveniles in the matriline increased, while females either showed no change or increased in condition. These sex-specific patterns suggest that males may receive reduced investment through prey sharing in families with more dependent young. Additionally, we found a negative relationship between the body condition of adult females and the number of offspring they have, indicating that adult females may also incur costs in provisioning offspring. Interestingly, these patterns did not depend on salmon abundance. Our results demonstrate how sociality can influence individual health and provides insights into intragroup conflict and parental investment in a species with lifelong parental care and high social stability.

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Acknowledgements

I did not expect to go to grad school. Doing my master's and learning to be a researcher was something I thought of, but never really believed would happen, especially not the way it has. Because of a community of people and support systems, I ended up getting accepted into school and working on a project which 20-year-old me would only dream of. Without this community I would have not gotten here nor had as much meaning and fun in my work.

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After 11 years of working on the water around charismatic megafauna and in exciting remote places, every year has left me with the same feeling: it's this community of people I cherish the most.

A54 matriline easting down the Johnstone Strait, by Sharon Kay January 2020.

Introduction

Animal social systems can become expansive, with many group members and diverse social roles. Group living strategies vary across taxa, where group living can be a temporary response to the environment (for example foraging aggregations), or where repeated association and social dynamics form to create long-term social units (Parrish et al., 1997, Krause and Ruxton, 2002). However, when resource availability becomes limited, intragroup competition can limit the extent to which an individual benefits from group living (Alexander, 1974; Rubenstein, 1978).

Social structures can mitigate competition between group members through fission-fusion dynamics when food becomes limited (Parker & Stuart, 1976; Silk et al., 2014; Chen et al., 2022). For example, grey wolf pack stability shifts seasonally where “extraneous” members split from the core group due to low prey density (Jordan et al., 1967; Sells et al., 2022). For animals with multi-tiered social structures, resource limitation can trigger fission of higher tiered groups while lower tier structures made of related individuals remain stable (Wittemyer et al., 2005; Smith et al., 2008; Carter et al., 2013; Sutton, 2019). This flexibility in group membership can temporarily reduce intragroup competition. However, some social systems are less fluid and mitigate intragroup competition by other means.

An alternative to group fission is to actively provision certain group members while limiting the provisioning of others, particularity for groups that share prey. Decisions around who is prioritised depend on the value and dependency of group members; and in hierarchies, it also depends on which group members hold provisioning power (Boone, 1992; Smith & Holekamp, 2023). In hierarchal matrilines, spotted hyenas share access to carcasses with those that have higher status (Hofer & East, 2003) and only share with lower ranking males when a carcass is large enough to facilitate sharing regardless of rank (Tilson & Hamilton, 1984). This dominance-driven sharing is demonstrated in common ravens as well (Horn et al., 2024). Relatedness between members can also influence provisioning decisions, where close kin are provisioned over less related group members, as seen in human and other primate societies (Jaeggi & Gurven, 2013). Highly dependent members such as young may also be disproportionally provisioned when resources are scarce (Malcolm & Marten, 1982; Tizo-Pedroso & Del-Claro, 2018). In addition to a member's relatedness, status, or dependency on shared resources, reciprocal altruism can also drive provisioning strategies. In vampire bats, individuals are more likely to share regurgitated food with group members that they had received food from in the past (Wilkinson, 1984; Carter & Wilkinson, 2013). This multitude of factors influencing how resources are allocated among group members highlights the uncertainty around how resources are divided within groups across different social systems.

Effective conservation of social species should consider if and how resources are allocated within groups and if providers of shared prey or dependent members incur costs when resources are limited. In this thesis, I will examine if group composition affects prey sharing between group members, and whether certain members incur associated physiological costs in a species with exceptionally high social stability: the threatened Northern Resident killer whales (*Orcinus orca ater*). I will do so by 1) investigating whether social group composition affects individual body condition and 2) evaluating if a mother's body condition depends on her offspring number and sex, while accounting for prey availability. This work will examine the inherent challenges social groups face in sharing resources and managing intragroup conflict, and the extent to which resource limitation exacerbates these challenges.

Chapter One: Group composition and allocation of shared prey in Northern Resident killer whales

Introduction

The conservation and management of wildlife requires consideration of a suite of factors that affect population viability. Conservation efforts are often focused on resource limitation from overharvesting, loss of habitat, and other anthropogenic threats (Lascelles et al., 2014; Arthington et al., 2016; Johnson et al., 2017). However, intrinsic population characteristics can interact with these stressors to influence population dynamics. Social systems strongly influence survival and reproduction in group-living species (Chapman & Bourke, 2001; Smith et al., 2016; Brakes et al., 2019). Conservation and management efforts focused on species with long-lasting social connections should therefore consider their sociality and how environmental conditions influence social dynamics.

1.0 Intragroup conflict and resource scarcity

Considering sociality in conservation efforts is particularly important for species facing resource scarcity, including from human impacts, because it can lead to intragroup conflict. Specifically, when resources become scarce, intragroup competition can become more pronounced (Alexander, 1974; Rubenstein, 1978). For example, in group-living mountain ungulates, declines in vegetation caused by climate change can lead to aggression between groupmates (Fattorini et al., 2023). Moreover, reduced prey diversity can increase dietary overlap between group members and promote competition (Gómez-Campos et al., 2011). For species that share food among group members, social dynamics can be especially relevant during food limitation (Malcolm & Marten, 1982; Tilson & Hamilton, 1984; Bird, 1997; Tizo-Pedroso & Del-Claro, 2018), particularly when the physiological health and evolutionary fitness of some members depend on provisioning (hereafter ‘recipients’). Whereas previous work has focussed on the evolutionary benefits of prey sharing (ie, kin selection, informational exchange, and reciprocity in primates and vampire bats (Wilkinson, 1984; Jaeggi & Gurven, 2013)), associated costs may also be incurred for providers and dependent recipients.

2.0 Provisioning of offspring

Conflict around how much providers provision recipients is well illustrated in parent-offspring relationships. Under resource limitation, conflict of interest arises between parents and individual offspring over the degree of parental investment (described as ‘parent-offspring conflict’ (Trivers 1974)). When parents are faced with provisioning multiple offspring, they are predicted to reduce investment in those that are highly dependent, costly to maintain, and have low reproductive value (individuals that have lower reproductive success) (Trivers, 1972; 1974). Investment in older offspring may be favoured because they have higher reproductive value (for example, in species in which older males have greater mating success), have a higher probability of surviving to reproductive age, and therefore provide higher inclusive fitness benefits (Hamilton, 1964, Trivers, 1974). Older offspring also require less time to reach independence, reducing long-term parental investment (Dawkins & Carlisle, 1976). Greater parental investment in older offspring relative to younger offspring has been documented in birds, particularly with regard to predator defense (Andersson et al., 1980; Tryjanowski & Goławski, 2004; Redmond et al., 2009; Svagelj et al., 2012). In Galapagos fur seals (*Arctocephalus galapagoensis*), mothers nurse older offspring at the cost of their younger offsprings’ survival, especially when food is limited (Trillmich & Wolf, 2008). These patterns of parental investment highlight the balance parents must strike to maximize their reproductive success.

Costs associated with parental investment depend not only on the age of the offspring, but also on their sex. Theory suggests that the indirect fitness benefits of investing in offspring of one sex over the other depends on parental condition (Trivers and Willard 1973). When resources are limited, parental investment should be directed to daughters over sons. This is because the reproductive success of sons is generally more variable than the reproductive success of daughters, particularly for sexually dimorphic and polygamous species in which a few high-quality males dominate mating (Hewison et al., 1999; Cockburn et al., 2002) Therefore, parents should only invest in sons when there are enough resources to raise a high-quality son who can successfully compete with other males to sire multiple offspring. Diminished investment in males during resource limitation has been documented in precocial birds, small mammals, and wild and semi-domesticated ungulates (Clutton-Brock et al., 1982; Holand et al., 2005; Koskela et al., 2009; Lemons et al., 2012).

3.0 Social System of Resident Killer Whales

Resident killer whales (RKWs; *Orcinus orca ater*) have a rare social system, where both sexes remain in their natal matrilines for their whole lives and persistently share their salmonid prey. This lifelong nondispersal of both sexes has been documented in only four non-human species (Greenwood, 1980; Bigg et al., 1990; Amos et al., 1993; Park et al., 1998; Rodrigues et al., 2010) and offers an opportunity to examine parental investment in a highly stable animal society. Adult females are the primary providers, sharing up to 90% of their kills (Wright et al., 2016). Adult males share with their mothers and younger siblings but also continue to be provisioned by their mothers throughout their lifespan (Ford & Ellis, 2006; Wright et al., 2016). RKW adult females might be challenged by providing for offspring of varying ages and energetic needs due to this lifelong parental investment. These challenges may be exacerbated by prey limitation, given that RKWs are limited by the abundance of their salmonid prey (Ward et al., 2009; Ford et al., 2010b; Vélez-Espino et al., 2015; Couture et al., 2022; Nelson et al., 2024). As a result, with increased conflict under food limitation, adult females might allocate resources unevenly among their dependent offspring to maximise inclusive fitness as predicted by parent-offspring conflict theory.

It is well-established that social group composition can influence the survival of RKW group members, which may have implications for long-term population dynamics (Foster, et al., 2012b; Croft et al., 2017; Ellis et al., 2017; Weiss et al., 2023). Here, we assess whether social group composition also affects shorter-term measures of health by examining the body condition of RKWs (Fearnbach et al., 2018, 2020). Body condition is affected by the amount and quality of prey consumed, regardless of whether those prey are obtained directly by foraging or is provided by mothers or other group members. Regarding provisioning, we reason that low body condition may reflect both the cost of providing shared prey to others and a lack of receiving from others. Although body condition measures physiological markers of health rather than individual fitness, these short-term markers could serve as yearly proxies for fitness because they are associated with annual survivorship in RKWs (Stewart et al., 2021). Given that such a metric integrates provisioning, evaluating body condition under various individual, social, and environmental (i.e. prey) contexts could not only shed light on parent-offspring and intragroup conflict but also provide timely management-relevant information on killer whales.

4.0 Research Aims

To examine how the composition of matrilines influences the body condition of matriline members, we analyzed a 10-year data set of aerial images of Northern Resident Killer Whales (NRKW), a population of approximately 350 individuals ranging from Southern British Columbia to Southeastern Alaska (Alert Bay Cetological Society, 2022; Ford, 2006). Specifically, we investigated how matriline composition by age-sex class may influence the body condition of their members, especially recipients, while accounting for salmon abundance. Because RKWs share prey among group members, we hypothesized that an individual's health depends on the social composition of their matriline. We predicted that individuals in matrilines with a higher proportion of juveniles and higher proportion of adult males have lower body condition due to the high dependency on provisioning and caloric needs of these members (Noren, 2011; Wright et al., 2016). Moreover, we predicted that individuals in matrilines with higher total caloric requirement and more group members exhibit lower body condition. We also hypothesized that when groups have many dependent members, provisioning is reduced to individuals that are most dependent, most costly to provide for, and have the lowest reproductive value. Accordingly, we predicted that the body condition of juveniles and adult males would be negatively associated with the proportion of dependents in the matriline, given that both are heavily provisioned by their mothers, juveniles have low reproductive value, and that adult males have high caloric requirements (Noren, 2011; Wright et al., 2016,). As an additional prediction, older adult males won't not show lower condition, given that they have high reproductive success and their high inclusive fitness value to mothers could outweigh costs from provisioning them (Barrett-Lennard, 2000; Ford et al., 2011, 2018). Finally, we expected that any negative associations between body condition and matriline composition to be more pronounced during years of lower salmon abundance, especially for male offspring (Trivers and Willard, 1973, Clutton Brock et al., 1985).

Methods

1.0 Field Data Collection

We sampled coastal British Columbia, Canada, along Northeastern Vancouver Island within Kwakwaka'wakw territories, and the Central Coast within Gitga'at, Kitasoo/Xai'xais, Heiltsuk, and Wuikinuxv territories (Figure 1). These are key summer foraging locations for NRKWs and within their critical habitat (Nichol & Shackleton, 1996; Ford, 2006).

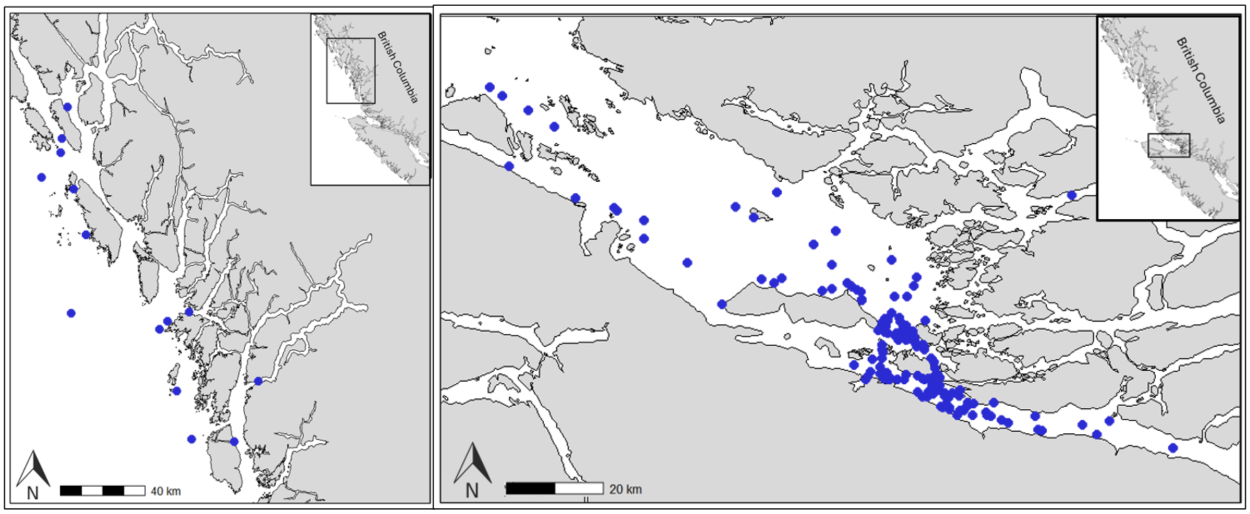


Figure 1. Central coast (left) and Northeastern Vancouver Island (right) study areas. Blue dots indicate location of encounters with Northern Resident killer whales from 2014 to 2023. Locations denote coordinates from position during the start of an encounter

Each summer from 2014 to 2023, we conducted approximately three to five-week field seasons in Johnstone Strait (August and September). We added two-week field seasons on the Central Coast in June 2019, July 2022, and July 2023. We conducted field work during summer months to avoid potentially confounding seasonal effects on body condition (Fearnbach et al., 2020) and to capture annual snapshots when body condition is likely highest (Stewart et al., 2021). All field activities were carried out under research permits XMMS-6-2014 (2014-2017), SARA permit held by Thomas Daniol-LaCroze (2018), XMMS-4-2019 (2019-2021) and XMMS-2-2022 (2022-2023) from Fisheries and Oceans Canada.

We searched for NRKWs via continuous visual and intermittent acoustic scans during daylight hours. From 2014 to 2022, we used an 8.2m motor vessel with a 2.5m top deck viewing platform, and in 2023 we used a 20m sailing vessel with a 5m viewing platform. We performed acoustic scans using a hydrophone with a ~10 nautical mile acoustic range during visual scans when weather conditions allowed. Our search efforts were guided by sightings information received via radio from local mariners, including whale watch operators, ecotour operators, coastal First Nation stewards, research outposts, and lighthouse keepers. Once we encountered NKRWs, we obtained lateral images by approaching the whales at 30-100 meters. While a vessel operator matched the speed and direction of whales, a photographer used a DSLR camera with a telephoto lens (300mm and 400mm maximum range) to capture high resolution photographs of the whale's flank and dorsal fin. These lateral photographs served the dual purpose of confirming which whales were present during the encounter and aiding in identification from same-day aerial images of whales during RPAS operations. Both these identification processes cross-referenced photo identification images from Department of Fisheries and Oceans Canada catalogues (Bigg, 1982; Towers et al., 2015, 2020)

To evaluate body condition of NRKWs from aerial photographs, we used Remotely Piloted Aircraft Systems (RPAS or 'drones') following protocols established by Durban et al. (2015). Aerial photographs were captured using several equipment systems as technology evolved over the study duration: an Aerial Imaging Solutions APH-22 hexacopter and Olympus E-PM2 camera with a 25mm F1.8 lens from 2014 to 2017, a DJI Matrice 200 quadcopter and Zenmuse X5S camera with a 25mm F1.8 lens from 2018 to 2022, and a DJI Inspire 3 quadcopter and Zenmuse X9-8K camera with a 24mm F2.8 lens in 2023. Our approach involved a dual controller system in which a camera operator captured images and directed the pilot with verbal commands to position the RPAS above the whales, while the pilot maneuvered the RPAS and maintained visual line of sight. The RPAS flew at 30 to 40 meters above the whales, with a gimbaled camera oriented at 90 degrees and parallel to the surfacing whales. A polarized filter was used to reduce glare from the sea's surface and camera settings ranged from F2.8 to 5.6 aperture, 400 to 3200 shutter speed, and 200 to 3200 ISO, depending on RPAS camera model and light conditions. Over the ten years of field work, the research team conducted 789 RPAS flights during 177 encounters with NRKWs. We photographed 219 individual whales from 42 matrilines during the study, with 133 whales sampled in multiple years and an average of 63 whales sampled in each year.

Our procedure was designed to minimize potential disturbance to whales. To our knowledge, killer whales have not demonstrated avoidance responses to RPASs, but other delphinids have shown evasive behaviours when approached by drones flying at less than 23 meters altitude (Aubin et al., 2023). Accordingly, we took precautions following recommendations from Durban et al. (2015), Raoult et al. (2020) and (Aubin et al., 2023): maintaining RPAS altitude at a minimum of 30m and monitoring for avoidant behaviours. Although we frequently conducted multiple flights over individual whales to ensure an adequate number of images for photogrammetric analysis, we limited total flight time over an individual whale to one hour per encounter. During RPAS operations, the vessel remained within 400 meters of the whales, moving slowly behind or parallel to them. To reduce vessel noise and disturbance, we minimized acceleration and sudden changes in direction.

2.0 Photogrammetry Analysis

We selected aerial images suitable for photogrammetric analysis based on clarity, resolution, and whale position. These criteria included images where the whale's eye patches were in focus, each end of the eye patches was visible above the water surface, and the whale had no discernable tilt in body axis or head. We assigned image quality on a graded scale from 1 (low quality) to 3 (high quality), considering the clear distinction of the edge of the whale's eye patches and any water distortion.

We estimated each whale's body condition by measuring the whale's eye patch ratio (Fearnbach et al., 2020). The eye patch ratio has been used as a proxy for the nutritional status of killer whales and reflects seasonal changes in body condition. Lower values indicate less fat behind the cranium, which is associated with increased probability of mortality (Fearnbach et al., 2020; Stewart et al., 2021). Using the software ImageJ (2023), we measured the distance in pixels between 1) the anterior tips of the whale's eyepatches and 2) the eyepatches at 75% of their length toward the posterior end (Figure 2). We then calculated the eyepatch ratio using the formula:

$$\text{Eye patch ratio} = \frac{\text{Distance between 75\% length of eye patches}}{\text{Distance between anterior edges of eye patches}}$$

We calculated the annual mean eye patch ratio for a whale using all suitable images from that sampling year. For whales with images from both study areas, we pooled images from both areas to calculate their annual mean eye patch ratio, as study area had no effect on eye patch ratio (See Supplementary Methods, Supplementary Figure 1).

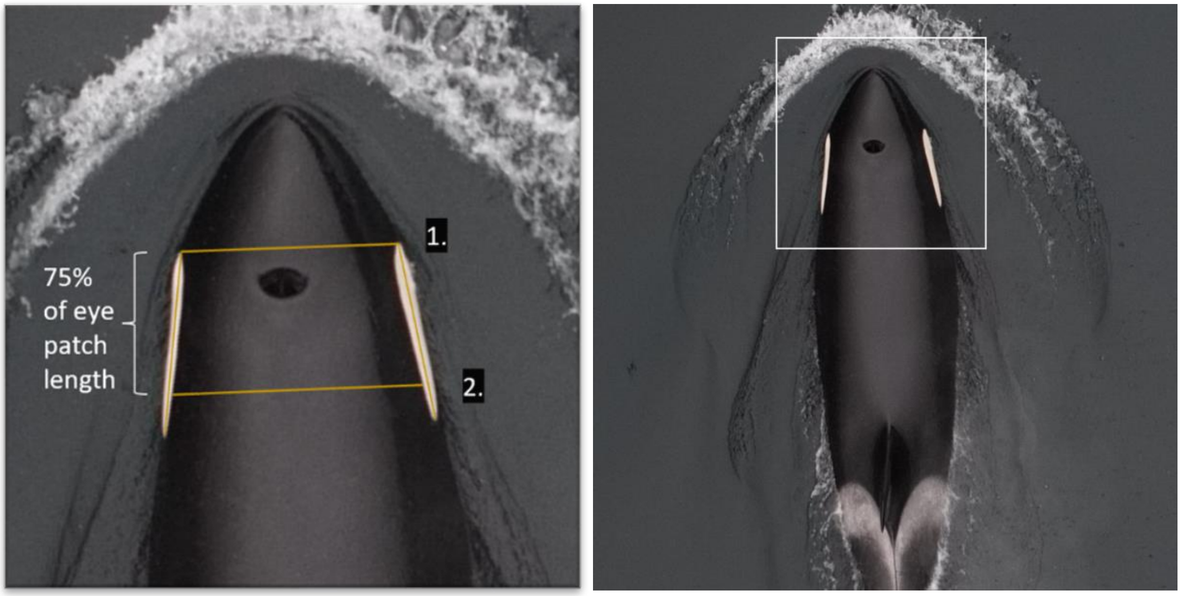


Figure 2. Example image of a high quality (scale 3) eye patch photograph of Northern Resident, I51. Measurements include 1) the distance between the anterior tips of the eye patch, and 2) the distance between the inner edges, 75% along the eye patch length towards the posterior end (methods from Fearnbach et al., 2020)

Eye patch ratio values tend to vary between 1.0 to 1.3 for RKWs (Stewart et al., 2021), so we accounted for uncertainty in these fine scale measurements. We measured each image twice, and the resulting values were averaged to calculate an eye patch ratio. Repeat measurements on an individual whale in a given year yielded an average coefficient of variation of 0.0112, ranging between 0.0002 and 0.0310. To examine potential outliers, we plotted raw eye patch ratio measurements for each whale per year. If an outlier was measured from a quality grade 1 image, we removed the value before calculating a whale's annual mean eye patch ratio.

Four people performed photogrammetric measurements depending on the year of data processing. To ensure that eye patio measurements were consistent across measurers, we tested between-measurer repeatability. Each measurer measured the same set of 30 aerial images. Using the Inter-class correlation coefficient (ICC) (Revelle, 2024) to compare observer measurement results. An ICC value of 1.0 and a $p\text{-value} < 0.05$ indicates perfect similarity between observers. We found high repeatability across observers ($ICC = 0.97$, $p < 0.001$), suggesting that differences between measurers were negligible.

3.0 Covariate Data

For each year of data collection, we obtained age, sex, matriline membership, birth year, and death year (if applicable) for every whale in our dataset from historical Department of Fisheries and Oceans Canada catalogues of NRKWs (Towers *et al*., 2015; 2020; Alert Bay Cetological Society, 2022). We designated matriline membership based on matriline classification from Department of Fisheries and Oceans Canada catalogues (Towers *et al*., 2015; 2020). Matriline members typically consisted of living descendants of one matriarch (dead or alive), with occasional exceptions where whales left their natal matriline to travel with others. If a whale was repeatedly observed travelling exclusively outside their natal matriline for over a year with another matriline (seemingly their adoptive matriline), we used the adoptive matriline as their matriline ID (Jared Towers, *personal communication*, November 10, 2023). In cases where a whale changed matrilines during the study period ($n = 2$; A94 and C31), the matriline assignment was adjusted for the year of the switch and thereafter.

To evaluate the potential role of matriline size and group composition, we calculated the following covariates: the number of whales in the matriline, the proportion of juveniles (age 3 to 11), the proportion of adult males (age 12 and above), and the proportion of adult females (age 12 and above) within the matriline according to age-sex class assignments from Olesiuk et al. (2005) and Wright et al. (2016). We used these covariates to account for varying levels of dependency on prey sharing or the likelihood of sharing within the matriline based on age-sex class from Wright *et al*., (2016). We did not include the proportion of calves as a covariate (age 3 and under) as these members are energetically dependent on nursing, not only on provisioning through prey sharing. We decided to evaluate candidate models without this covariate to simplify our model set and only include models that addressed costs of provisioning through prey sharing. We also considered the total caloric requirement of each matriline as a social variable. We used daily caloric requirement estimates (kcal/day) of NRKW from (Noren, 2011) based on age and sex of a whale. We then summed the caloric requirements of individual matriline members to calculate the total daily caloric requirement of a matriline during a given year of the study.

We accounted for prey availability using abundance estimates of the primary prey of NRKWs, Chinook salmon (*Oncorhynchus tshawytscha*) (Ford and Ellis, 2006). We used the Pacific Salmon Commission's annual ocean catch abundance indexes from 2014 to 2023 (Chinook Technical Committee, 2023), which estimates salmon abundance relative to levels measured in 1979-1982. This metric has been show to correlate with NRKW mortality and fecundity (Ward et al., 2009; Ford et al., 2010b). Additionally, interactions between the abundance index and social factors have been found; lower social connectivity and lack of matriline leadership results in higher mortality when salmon abundance is low (Foster et al., 2012; Brent et al., 2015; Ellis et al., 2017). We averaged the annual abundance indexes across three areas, Southeastern Alaska, Northern British Columbia, and West Coast Vancouver Island, as the NRKW range includes all three areas (Ford, 2006).

Harvest data do not directly measure prey available for NRKW; instead, they measure the amount harvested and thus no longer available to NRKWs to forage. However, the premise of the index is that the quantity of fish harvested by ocean fisheries is proportional to the abundance of fish in the environment (Chinook Technical Committee, 2023), and thus is likely proportional to the abundance of fish available for NRKW.

4.0 Statistical Analysis

Using the programming software R 4.2.3 (R Core team, 2023), we conducted statistical analysis to investigate how NRKW body condition might be associated with group composition (while accounting for salmon). We constructed a set of 10 candidate models (n = 596) based on *a priori* hypotheses (Supplementary Table 1). For each model we fit the data with linear mixed effects models and a Gaussian distribution using the R package glmmTMB (Brookes *et al.*, 2017).

To address how individual body condition is associated with matriline composition, we competed models with social covariates and individual level covariates. The social covariates included the proportion of juveniles in the matriline, proportion of adult males, proportion of adult females, matriline size, and the estimated daily caloric requirement of the matriline. Each model included an age term fit with a cubic natural spline (df = 3) (R core team, 2023) to address non-linear allometric patterns in eye patch ratio (Stewart et al., 2021). We also fit our matriline size covariate with a cubic natural spline (df = 2) as functions of killer whale group size can be non-linear (Baird & Dill, 1996). For individual level covariates, our models included the whale's age and sex to account for variation in body condition as males and females mature (Stewart et al., 2021). We included interactions between age, sex, and all social variables, as the relationship between social covariates and body condition may depend on the whale's age-sex class due to distinct age and sex-specific social roles within the matriline. We only included whales with known sex for this analysis (removed n = 39 observations). We also included models with a salmon and social covariate interaction term to address the potential influence of food availability on social factors. We used whale identity and matriline identity as random effects to account for individual and group level variation and included an autoregressive term to account for correlation between measurements of the same individual from successive years (Pinheiro et al., 2023).

We evaluated model selection using the Akaike Information Criteria (AIC; Anderson & Burnham, 2002), considering models within 2 AIC points of the top performing model (lowest AIC) as competitive, unless simpler models had lower ΔAIC (the difference in AIC between each model and the best model) than more complex models (Anderson & Burnham, 2002; Arnold, 2010). We validated model performance using the R package DHARMa (Hartig, 2022), and assessed covariate strength by evaluating coefficients and their 95% confidence intervals within our top models. We also computed relative variable importance (RVI) values for each term in our top models to understand which variables had the strongest predictive influence on body condition.

Results

From the 10 sampled years of NRKW body condition data, we analyzed 557 observations from 175 individuals (0.99 – 1.29 range in eye patch ratio). At the individual level, males had higher eye patch ratios than females, and older individuals had higher eye patch ratios than younger ones (Figures 3-4). After accounting for these individual level variables, we found evidence that social covariates influenced body condition. Our analysis indicated the proportion of juveniles in the matriline was the most important social predictor (inferred by AIC and RVI values). The influence of our salmon covariate on body condition was minimal; we observed a slight but negative association (the smallest among all variables with coefficients for which the 95% confidence intervals did not overlap zero; Figure 3, Supplementary Figure 2), and no interaction term that included salmon was significant (Supplementary Figure 3).

Multi-model inference suggested that a simple model, containing only the proportion of juveniles as a social correlate, performed the best (AIC weight 0.58, Table 1). This model accounted for 85% of the variation in the data, with 42% of the variation explained by fixed effects. Across models, the proportion of juveniles was four times more important in predicting eye patch ratio (RVI = 0.39) than the proportion of adult males (RVI = 0.09), and at least 39 times more important than the proportion adult females (RVI = 0.01), matriline caloric requirement (RVI = 0.00), and matriline size (RVI = 0.00) (Supplementary Table 2).

While our top model indicated that the proportion of juveniles in the matriline predicted eye patch ratio, this relationship depended on the whale's age and sex (Figures 3, 4). The proportion of juveniles in the matriline was positively associated with body condition for older adult females (age 32, slope = 0.035, 95% CI: 0.004 to 0.066) This relationship was weaker and nonsignificant for young females (age 5, slope = 0.012, 95% CI: -0.019 to 0.043) and mid-aged females (age 18, slope = 0.005, 95% CI: -0.021 to 0.032; Figure 4). For males, the proportion of juveniles was negatively associated with body condition for all age groupings. The strongest negative association was found in mid-aged males (age 18, slope = -0.048, 95% CI: -0.075 to -0.021), then juvenile males (age 5, slope = -0.042, 95% CI: -0.072 to -0.011), with the weakest association for older males (age 32, slope = -0.018, 95% CI: -0.054 to 0.017) (Figure 4).

Table 1. Model selection results (n = 557 observations, 175 individuals). Models varied by which social covariate was included (indicated in 'social covariate' column), and whether salmon abundance was also considered in interaction terms with the social covariate (denoted by an x). For each model, the social covariate it contained was also considered in interaction terms with age and sex. See Supplemental Table 1 for full list of terms for each model in the model set. The top performing models and any competitive models (see Methods) are indicated in bold font. K indicates the number of terms in the model including

each degree of any natural spline covariate and interactions with natural spline covariate, as well as the autoregression term for temporal autocorrelation in year body condition measurements (K = 2)

Model #	Social covariate	K	AICc	Δ AICc	AICc Weight
3	**Proportion juveniles**	**18**	**894.88**	**0.00**	**0.58**
4	Proportion juveniles x salmon	19	896.96	2.08	0.20
5	Proportion adult males	18	897.73	2.85	0.14
6	Proportion adult males x salmon	19	899.86	4.98	0.05
1	Proportion adult females	18	901.69	6.82	0.02
2	Proportion adult females x salmon	19	903.65	8.78	0.01
7	Matriline caloric requirement	18	905.73	10.86	0.00
8	Matriline caloric requirement x salmon	19	907.81	12.93	0.00
9	Matriline size	23	915.32	20.44	0.00
10	Matriline size x salmon	25	918.79	23.91	0.00
Null	None	6	1063.86	168.98	0.00

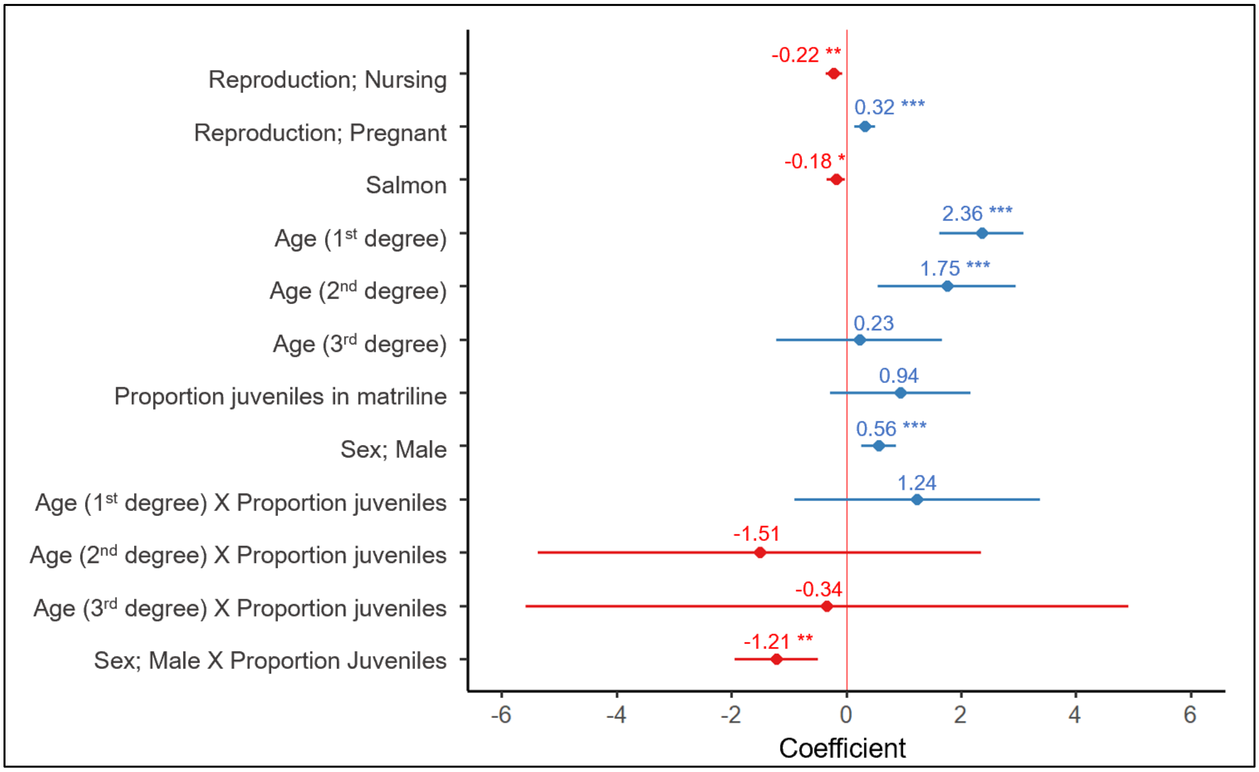


Figure 3. Coefficients (dots) and 95% confidence intervals (lines) for fixed effects in the top performing model (model #3) for predicting eye patch ratio among all age sex classes. Symbols denote P values (*** = 0.0001, ** = 0.001, * = 0.01, · = 0.05). Blue values indicate positive associations and red values indicated negative associations between predictors and eye patch ratios. Categories denoted by ‘;’ represent level of the predictor variable compared to the base case level. Brackets around age terms represent the degree of natural spline function for age

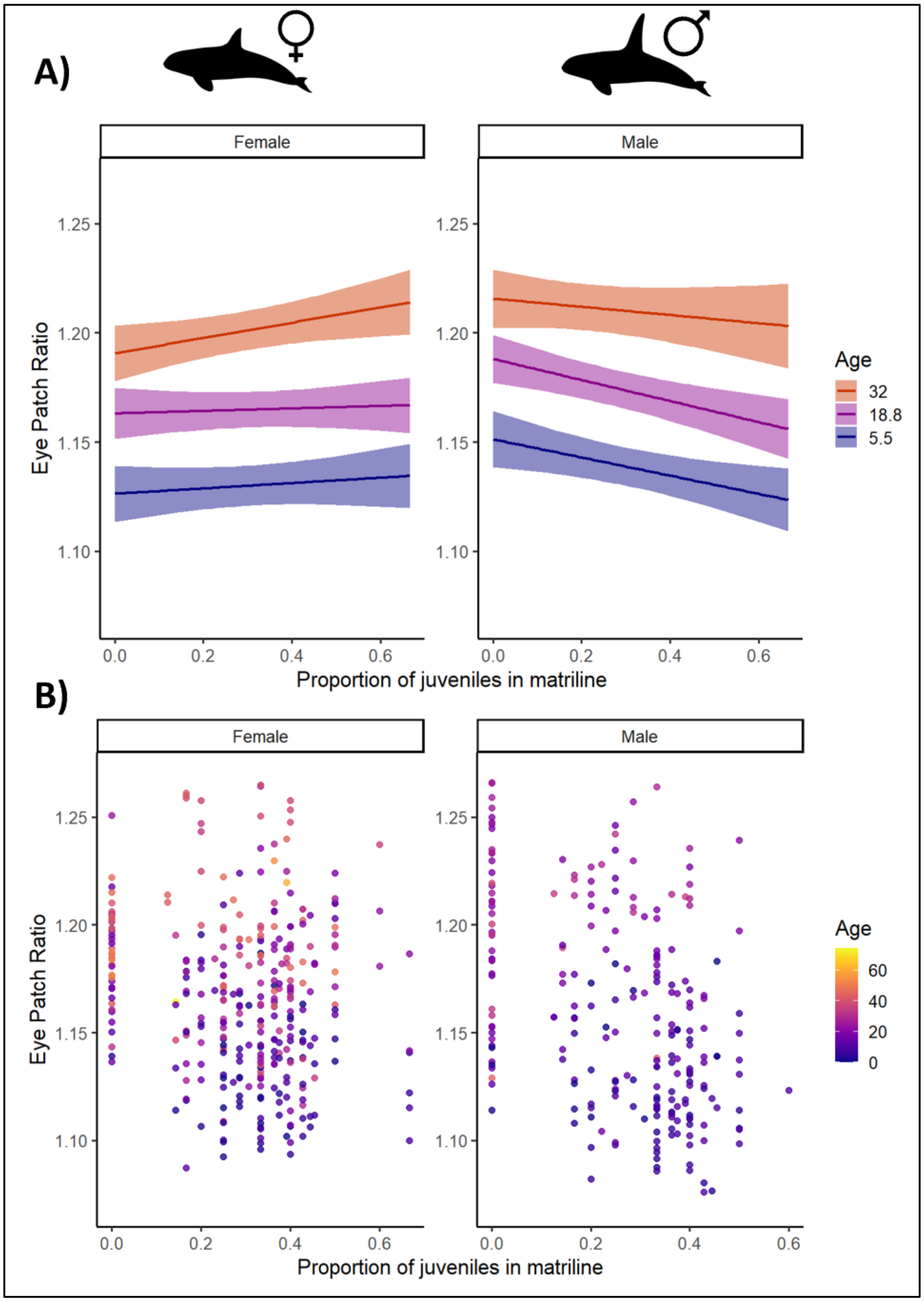


Figure 4. Top performing model in the model set (model #3) for all age and sex classes. A) Predicted eye patch ratio values by age and sex as a function of the proportion of juveniles in matriline. All other model terms are held at mean values. Age is represented visually as three categories: the mean age of NRKW in the data set (18.5), mean age plus one standard deviation (31.7), and mean age minus one standard deviation

(5.4). Lines represent model predicted values and shaded areas represent 95% confidence intervals. B) Raw data showing range of eye patch ratio values for NRKWs in association with the proportion of juveniles in matriline, according to age and sex of whales

Discussion

Our results illustrate how group composition can influence the nutritional status of individuals living in groups. Specifically, we found that males within matrilines with a high proportion of juveniles showed lower body condition than males within matrilines with few juveniles, a pattern not observed in females. Immature and teenage males showed the strongest negative associations. Contrary to our expectations, these relationships did not appear to be influenced by chinook salmon abundance during the years of this study. These results suggest that the composition of killer whale matrilines could influence individual health regardless of prey abundance, particularly when groups have many dependent members. The contrasting relationships between body condition and the proportion of juveniles in the matriline in males and females could indicate that, when providers have many dependents to feed, they decrease provisioning of males, but not females.

1.0 Limitations

Our approach carries several limitations. For one, our interpretation is constrained by the inability to distinguish the relative contribution of prey sharing and foraging ability of recipients in shaping their nutritional condition. Low body condition could reflect insufficient provisioning of recipients, over expenditure of provisioning by providers, or poor foraging ability. We reason, however, that low condition could indicate that the provisioning a whale received did not compensate for any shortcomings in foraging. Using a whale's eye patch ratio to reflect individual body condition and health also presents challenges. While these measurements have been linked to the survival and nutritional status of killer whales (Fearnbach et al., 2020; Stewart et al., 2021), morphometric data reflecting blubber loss along a whale's entire body might have more predictive power (Christiansen et al., 2016, 2019; Hogg et al., 1992; Castrillon & Bengtson Nash, 2020; Arranz et al., 2022).

2.0 Effects of group composition on body condition depend on sex and age

Despite these limitations, our results suggest that males, particularly immature and teenage males, may receive reduced provisioning when there is a high proportion of dependents in the matriline. In mammals, higher costs of provisioning males begin at the onset of post-parturition maternal investment because nursing rates are often higher in males (Clutton-Brock et al., 1981; Hogg et al., 1992; Birgersson et al., 1998). In killer whales, which receive life-long maternal investment through prey sharing, these costs may peak when males grow rapidly during their teenage years (Noren, 2011). Our results align with this interpretation because teenage males had the strongest negative association between body condition and the proportion of juveniles in their matriline. The pronounced long-term costs of sons is evident in RKWs; a female's lifetime reproductive output is limited if she has a son (Weiss et al., 2023). Our results support the idea that NRKW sons are costly to maintain, given that providers (mainly adult females, Wright et al., 2016) might reduce investment in immature and teenage males under more challenging social group composition.

In contrast to patterns observed among younger males, we found that in older adult males, body condition had little association with the proportion of juveniles in their matriline. Such a pattern could arise via two non-exclusive pathways. One pathway is that older males are better foragers and less dependent on prey sharing than younger males. Older males could be more experienced at finding prey, making them less dependent on provisioning. Moreover, the larger size of older males allows them to dive deeper and expand their foraging niche (Beerman et al., 2016), although their size could reduce the agility required to catch salmon (Blanckenhorn, 2000). As an additional pathway, older males might show weaker association between body condition and the proportion of juveniles in their matriline because they continue to be provisioned irrespective of the number of juveniles. Evidence suggests that older adult males are provisioned by adult females (Wright et al., 2016) and those without mothers spend more time foraging than those with mothers (Tennessen et al., 2023). If older males are provisioned despite social constraints while younger males receive reduced investment, the higher reproductive value of adult males may explain why. In many mating systems, older males often have higher mating success (Fiske et al., 1998; Alonso et al., 2010; Brooks & Kemp, 2001), including in RKWs (Barrett-Lennard, 2000; Ford et al., 2011, 2018). Investing in older males might incur greater inclusive fitness benefits because they have less variable mating success, have already survived to sexual maturity, and therefore are of higher reproductive quality (Trivers, 1972, 1974).

Interestingly, older adult females showed a positive association between body condition and the proportion of juveniles in their matriline. We expected a weak or negative association, depending on whether females reduced provisioning to recipients or incurred costs from providing for many dependent juveniles. We note that the proportion of one age sex class within a matriline is inherently correlated with the proportion of another (although our candidate model set did not consider these variables together in any model). Accordingly, this unexpected positive association for older adult females might be due to a negative correlation between the proportion of juveniles and proportion of adult males in a matriline. Our lower ranking models indicated that older adult females had lower body condition in matrilines with more adult males, suggesting confounding effects might explain the unexpected positive association. The proportion of juveniles was also negatively correlated with the proportion of calves in the matriline. Therefore, adult females might have higher body condition in matrilines with more juveniles because they are less likely to be nursing their own calf, which reduces their body condition (Amy Rowley, unpublished data). However, if this release from nursing explains why adult females have higher body condition in matrilines with more juveniles, we would also expect mid-aged females to show a negative relationship, but they showed no association.

3.0 Proportion of adult males in the matriline and salmon abundance are not strong predictors of body condition

Contrary to our expectations, the proportion of adult males in a matriline was not a strong predictor of individual body condition. Our modeling approach might in part explain why. We combined the proportion of teenage and older adult males into one variable (proportion adult males) to reduce model complexity, a scenario that may obscure their different social roles and abilities. As previously stated, older adult males might not be as costly to maintain through provisioning as initially thought (Wright et al., 2016; Stredulinsky et al., 2021). However, the proportion of teenage males could be an important predictor of body condition, given our results suggesting they are most sensitive to group composition and possible reduction in provisioning. Younger adults still require skill development, need to search wider ranges for prey, and are less successful at capturing larger prey compared with older adults (Desrochers, 1992; Sand et al., 2006; Penteriani et al., 2013). Additionally, older males might even support their matrilines by babysitting their younger siblings (Waite, 1988, Bisther and Vongraven, 1993), a role teenage males may not perform. Therefore, future studies could examine teenage and older males separately when considering social interactions with RKW sex classes, should statistical opportunity permit.

We found a weak relationship between salmon abundance and NRKW body condition (alone or in any interaction), which has at least two possible non-exclusive explanations. One, there might have been abundant salmon to meet the needs of NRKWs during the years of this study. Despite considerable variation in salmon abundance, the lowest abundance during our study was 37% higher than the lowest recorded during Ford et al.'s (2010b) study that indicated NRKW survival is negatively associated with chinook salmon abundance. Possibly, the minimum salmon abundance during the 10 years of our study was sufficient for the whales to avoid adverse effects on body condition. As an alternative, the Pacific Salmon Commission's chinook abundance index may not accurately reflect the availability of prey for NRKWs. Measures of body condition can be sensitive to seasonal shifts in prey abundance (Fearnbach et al., 2020), and the annual abundance index's temporal scale may not reflect seasonal variation in chinook abundance. Additionally, the index's geographic range may not adequately measure the abundance of specific salmon stocks important to NRKWs (Ford & Ellis, 2006, Ford et al., 2010a). Finer geographic measures of chinook abundance have been related to NRKW survival and fecundity during years prior to our study (Vélez-Espino et al., 2015). However, during our study period, the cumulative trend of these fine scale estimates paralleled the abundance index trend and might similarly predict body condition.

Other social and ecological considerations about salmon abundance might also be relevant. Given that males showed lower condition in matrilines with more juveniles independently of salmon abundance, our results suggest that salmon is not being adequately shared when providers are challenged by provisioning many dependent members. This suggests that the abundance or quality of salmon might be limited since certain recipients are not receiving consistent provisioning under certain group compositions. Finally, in addition to abundance, the quality and size of individual salmon might limit RKWs (Couture et al., 2022), and further studies might consider prey size when examining effects of prey limitation.

4.0 Implications

Our findings indicate that matriline composition can significantly influence the body condition of certain NRKW age-sex classes, which suggests that social factors should be considered in their conservation and management. While we cannot change the group composition of NRKW matrilines, understanding the conditions that might mitigate these negative effects is important. If females are challenged with provisioning their many dependent group members, particularly young males, conditions that promote more cooperative provisioning could reduce these costs. Post-reproductive matriarchs continue to provision group members, particularly their adult sons (Wright et al., 2016) and are less likely to have their own juvenile offspring to care for. When matrilines are faced with provisioning many dependent members, these older females might help cooperatively provision dependent matriline members given that nonbreeding helpers are primary providers in other cooperative species (Clutton-Brock et al., 2004; Forssman et al., 2018). As well, older individuals promote reproductive and foraging success among their relatives, as demonstrated in African elephants (*Loxodona africana*), and importantly, resident killer whales (McComb et al., 2001; Brent et al., 2015). Therefore, promoting longevity in NRKW matriarchs by increasing prey availability in conjunction with reduced noise pollution and chemical contaminants (Williams et al., 2024) could facilitate more cooperative and effective prey sharing throughout matrilines. Additionally, the RKW Recovery Strategy emphasizes that the presence of intact RKW matrilines allows for “cultural continuity” and is an important factor in population recovery (Fisheries and Ocean’s Canada, 2018). Results from this work supports this notion, as promoting conditions that support intact matrilines with long-lived members could reduce competition for their limited prey.

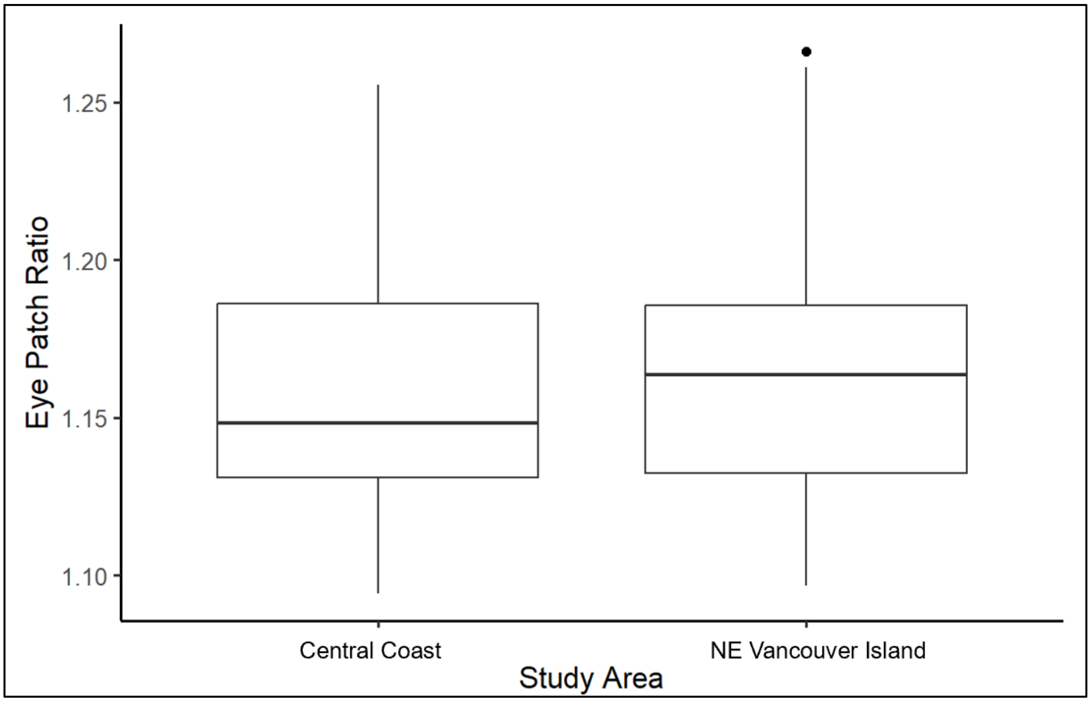
More broadly, our work highlights how conflict over parental investment can occur in a system with nondispersal of offspring from their natal groups. We show that young males may receive less provisioning than females of the same age when social groups have many dependent members. We also find that maternal providers may invest preferentially in older adult males rather than younger males when social group composition challenges adequate prey sharing. This suggests that the reproductive value of a group member can outweigh the cost of fulfilling its high caloric needs. In conclusion, our study reveals complex patterns of resource allocation in a stable social system and suggests that the health of group members depends on not only ecological factors, but also their social environment.

Supplementary Material: Chapter One

Evaluating effect of area on body condition

As our field work on the Central Coast was conducted earlier in the summer than field work in Johnstone Strait, we considered the possibility of confounding seasonal differences in body condition between the two sites. To evaluate the effect of study area on body condition, we analysed the body condition of whales that were observed in both study areas in the same year (n = 80 observations, 36 individuals). We visualized the effect of area by plotting the raw data from whales with observations in the Central Coast and Northeastern Vancouver Island. We then evaluated the effect of study area using a generalized mixed effects model, which included the study area as a fixed effect, and matriline ID and whale ID as random effects. We fit the model with a Guassian distribution, following protocols from our main analyses.

We found area had little effect on body condition (Supplementary Figure 1). Our model indicated that body condition was not significantly different between areas (Coefficient = 0.004, Z value = 1.45, p value = 0.15).



Supplementary Figure 1. Eye patch ratio by study area (Central Coast and Northeastern Vancouver Island), n = 80 observations, 36 individuals. Box boundaries indicate the interquartile range (IQR) of values, between the 1st and 3rd quartile (Q1, Q3). Horizontal lines within the IQR represent the median value. Whiskers represent the minimum (Q1 – 1.5 x IQR) and maximum values (Q3 + 1.5 x IQR). Black does denote outliers

Additional Supplementary Material

Supplementary Table 1. List of non-abbreviated (i.e., all terms) candidate models (n = 557). All models included an additional autoregression term to account for temporal autocorrelation between measures of the same whale in subsequent years. Models 1-10 include random effect of whale ID and matriline ID

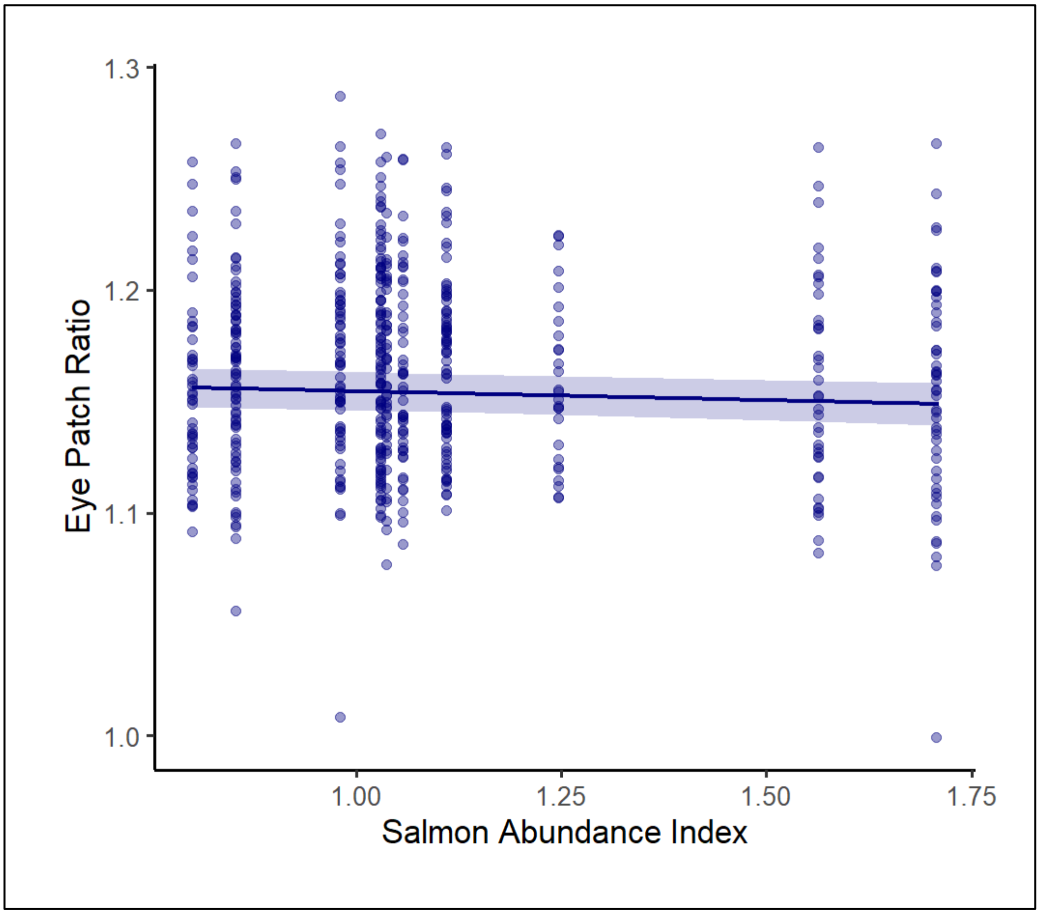
Null Model	
Null	1 + random effects (whale ID and matriline ID)
Proportion of adult females in matriline models	
1	Proportion adult females x age + proportion adult females x sex + salmon + reproductive status + age + sex

2	Proportion adult females x salmon + proportion adult females x age + proportion adult females x sex + salmon + reproductive status + age + sex
Proportion of juveniles in matriline models	
3	Proportion juveniles x age + proportion juveniles x sex + salmon + reproductive status + age + sex
4	Proportion juveniles x salmon + proportion juveniles x age + proportion juveniles x sex + salmon + reproductive status + age + sex
Proportion of adult males in matriline models	
5	Proportion adult males x age + proportion adult males x sex + salmon + reproductive status + age + sex
6	Proportion adult males x salmon + proportion adult males x age + proportion adult males x sex + salmon + reproductive status + age + sex
Matriline caloric requirement models	
7	Matriline caloric requirement x age + matriline caloric requirement x sex + salmon + reproductive status + age + sex
8	Matriline caloric requirement x salmon + matriline caloric requirement x age + matriline caloric requirement x sex + salmon + reproductive status + age + sex
Matriline size models	
9	Matriline size x age + matriline size x sex + salmon + reproductive status + age + sex
10	Matriline size x salmon + matriline size x age + matriline size x sex + salmon + reproductive status + age + sex

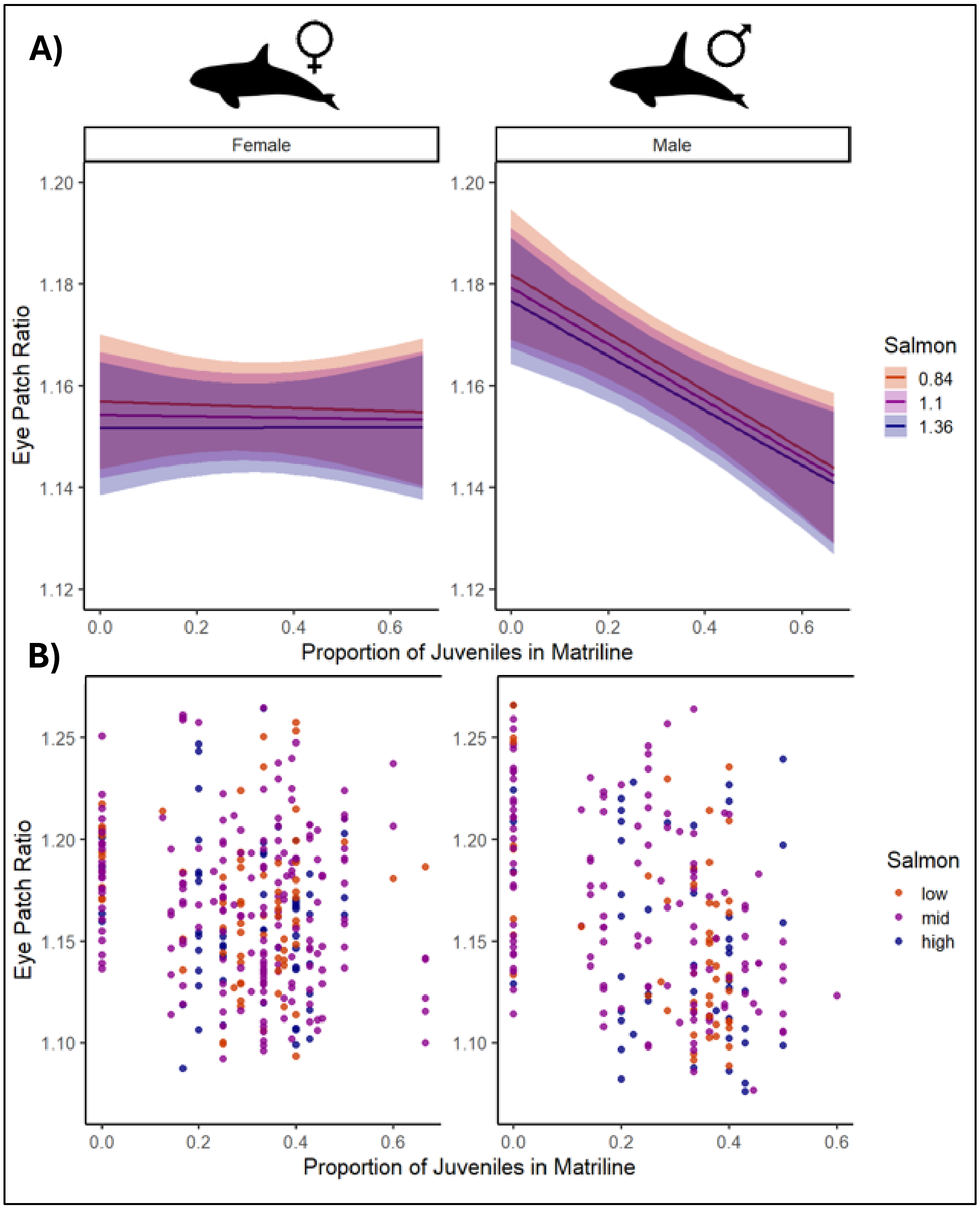
Supplementary Table 2. Relative Variance Importance factor (RVI) of social covariates and associated interaction terms our model set (n = 557). Individual level covariates such as age, sex, reproductive status, as well as salmon abundance are not shown because these terms were included in every model and thus their associated RVI is uninformative

Predictor Variable	**RVI**
Proportion juveniles	0.39
Age x proportion juveniles	0.39
Sex x proportion juveniles	0.39
Salmon x proportion juveniles	0.22
Proportion adult males	0.09
Age x proportion adult males	0.09
Sex x proportion adult males	0.09

Salmon x proportion adult males	0.05
Proportion adult females	0.01
Age x proportion adult females	0.01
Sex x proportion adult females	0.01
Salmon x proportion adult females	0.01
Matriline caloric requirement	0.00
Age x matriline caloric requirement	0.00
Sex x matriline caloric requirement	0.00
Salmon x matriline caloric requirement	0.00
Matriline size	0.00
Age x matriline size	0.00
Sex x matriline size	0.00
Salmon x matriline size	0.00



Supplementary Figure 2. Effect of salmon abundance on predicted eye patch ratio from top model. All other model terms are held constant at their mean. Blue line and shaded blue area indicate model predicted eye patch ratios with associated 95% confidence interval. Blue dots indicate raw data values of eye patch ratio across salmon abundance.



Supplementary Figure 3. Second ranking model (Δ AIC = 2.08) from model set on all age sex classes revealing the effect of proportion juveniles and salmon interaction term. A) Top panels indicate model predicted eye patch ratio values by sex and salmon abundance as a function of the proportion of juveniles in the matriline. The y axis scale is reduced compared to panel B to help visualize the lack of effect of salmon abundance and interaction with proportion of juveniles. Salmon abundance is represented visually as three categories (the mean abundance (1.10), mean abundance plus one standard deviation (1.35), and mean abundance minus one standard deviation (0.84). All other model terms are held constant at their mean. Lines represent model predicted values and shaded areas represent 95% confidence intervals. B) Bottom panels indicate raw data showing range of eye patch ratio values for NRKWs in association with the proportion of juveniles in matriline, according to sex and salmon abundance. Salmon abundance is categorized into three groupings; low, mid, and high, according to mean abundance +/- one standard deviation

Chapter Two: Cost of parental investment from life-long provisioning in Northern Resident killer whales

Introduction

1.0 Costs and strategies of parental care

Identifying the factors that limit reproduction and survival of breeding individuals is a critical goal in the conservation management of wildlife. Among the limitations are costs associated with parental care. Breeding individuals must successfully rear their offspring (increasing their reproductive success) at the cost of the parent's ability to invest in additional or future offspring, described as 'parental investment' (Trivers, 1972). Investment can start before conception through pre-emptive resource gathering (Boutin et al., 2000) and in some social taxa, continue even after offspring mature (Clutton Brock 1991). Early studies on parental investment showed that the degree of investment depends on offspring quality and independence (Trivers, 1972, 1974; Haig, 1990). Notably, greater investment is needed as offspring number and size increase, but excessive investment per offspring can reduce fitness for both parents and offspring, suggesting an optimal brood size for maximum fitness (Smith & Fretwell, 1974; Morris, 1987). Empirical evidence shows that increased brood size has trade offs such as reduced offspring mass, offspring survival, and may compromise a parents' future reproductive success, body condition, and survival (Hegner & Wingfield, 1987; Dijkstra et al., 1990; Olssen & Shine, 1997; Tarof et al., 2011; Koch & Meunier, 2014). These costs can be pronounced when resources are scarce, leading parents to produce smaller broods (Wiehn & Korpimäki, 1997; Beekey & Karlson, 2003). Much research on parental investment stems from work on birds and their yearly clutch (i.e., brood) sizes. Mammals, however, can incur unique costs and be burdened with longer investment periods.

In mammals, parental care during early offspring development can impose considerable investment costs. Pregnancy not only imposes energetic costs (Mover et al., 1988; Speakman, 2007), but can also require costly behavioural shifts. For example, pregnant northern elephant seals (*Mirounga angustirostris*) reduce their foraging dive depths, likely to allocate oxygen to their developing fetus (Hückstädt et al., 2018). Post-parturition investment can be even greater due to the high physiological costs of lactation (Clutton-Brock et al., 1989; Clutton-Brock, 1991). Nursing costs can be especially pronounced for mothers with sons, given the higher nutritional demand of males in species with male-biased sexual dimorphism (Clutton-Brock et al., 1981, 1985). The apparent higher cost of sons is supported by studies on maternal fitness, demonstrating that a mother's health and future reproductive output decline after raising an energetically costly son (Berube et al., 1996; Douhard et al., 2020; Weiss et al., 2023). Whereas some species only incur costs during these initial periods of investment, others continue to invest in their offspring up to and even beyond maturity.

In some social systems, parental investment is extended to the scale of lifetimes. This can take various forms. For example, the geographic range of offspring can overlap with their parents (Greenwood, 1980). Investment in this context can be modest, given that philopatric offspring gain access to local resources but independently garner them (Wasser, 1988; Moses & Millar, 1994). However, in some social systems, offspring continue to receive high levels of parental investment after nutritional independence, including predator defence, grooming, and even direct provisioning with shared food (Thiel, 2003, Noordwijk, 2012). In short, for highly social species with life-long parental investment, costs from parental care may be considerable to a parent's fitness.

2.0 Parental investment in Resident Killer Whales

Resident killer whales (RKW; *Orcinus orca ater*) invest in extensive parental care past weaning and even sexual maturity of their offspring, which may incur long lasting costs. At the onset of care, RKW females demonstrate a long reproductive investment period, with gestation lasting approximately 17 months (Walker et al., 1988) followed by approximately two to three years of nursing (Oftedal, 1997, Olesiuk et al., 1990, 2005). After weaning, parental care continues through lifelong sharing of their salmonid prey (Ford & Ellis, 2006; Wright et al., 2016). While adult daughters receive less provisioning as they age and raise their own offspring, adult males continue to be provisioned by their mothers throughout their lives (Wright et al., 2016). RKW mothers face especially pronounced costs from bearing male offspring due to this lifelong investment. Weiss et al., (2023) found that a mother's annual probability of producing a viable calf in subsequent years is reduced by 70% when she has a son compared to having only daughters, suggesting there are costs to provisioning sons with higher growth rates and nutritional demands. RKWs are further challenged in provisioning offspring as they are limited by their salmonid prey, as their fecundity, survival, and social structure depends on chinook salmon (*Oncorhynchus tshawytscha*) abundance (Ward et al., 2009; Ford et al., 2010b; Vélez-Espino et al., 2015; Foster et al., 2012; Stredulinsky et al., 2021; Couture et al., 2022; Nelson et al., 2024).

3.0 Research Aims

Given the potentially costly nature of RKW maternal care, we reason that a mother's body condition is influenced by the physiological costs associated with parental investment. Evaluating individual body condition has revealed the effect of reproductive costs in cetaceans (Christiansen et al., 2016; Vermeulen et al., 2023; Pirotta et al., 2024), and has been associated with nutritional status and survivorship in killer whales (Fearnbach et al., 2018, 2020; Stewart et al., 2021). Accordingly, our objective was to investigate how parental investment, including post-weaning care through the life-long provisioning of offspring, affects the body condition of RKW mothers. Specifically, we investigated the relationship between adult females' body condition and the number and sex of their offspring. To achieve this goal, we analyzed a ten-year data set of aerial images from which the body condition of Northern Resident Killer Whale (NRKW) individuals was measured yearly. We hypothesized that adult females incur costs from provisioning their nondispersing offspring and that male offspring incur larger costs to mothers than daughters (Weiss et al, 2023). We predicted that females with more offspring have lower body condition, and that mothers with sons have lower condition than those with only daughters (Weiss et al. 2023). Given the increased caloric requirements and continued dependency on parental provisioning of older males (Noren, 2011; Wright et al., 2016), we also predicted that mothers with an adult sons have lower body condition compared to mothers with only subadult sons. Because NRKWs are limited by prey abundance (Ward et al., 2009; Ford et al., 2010; Vélez-Espino et al., 2015), we predicted that any negative associations between a mother's body condition and her offspring's characteristics are be more pronounced during years of lower salmon abundance.

Our study provides new insights into the costs of parental care in species with long-term investment. Given the Threatened status of our study population (Species at Risk Act, 2003), we consider this applied research; our work will investigate whether prey abundance exacerbates these intrinsic costs, which has important implications for the conservation of NRKWs. In species with prolonged parental investment, the ability of females to care for their offspring is critical for their survival. Understanding how prey limitation affects the condition of mothers caring for multiple offspring will therefore be useful in determining what social and environmental factors influence survival in adult females and their offspring.

Methods

For detailed methods on field collection and photogrammetric analysis, see methods described in Chapter 1.

1.0 Covariates

Our analysis on the effects of provisioning costs to adult NRKW females, included demographic data, and annual estimates of salmon abundance. We complied demographic data from historical Department of Fisheries and Oceans Canada catalogues of Northern Residents (Towers *et al*., 2015; 2020; NRKW App, 2023). For each year of data collection, we derived age, sex, mother ID, birth year, and death year (if applicable), for every whale in our dataset. Using this demographic data, we constructed social covariates based on mother and offspring characteristics to investigate effects of provisioning demands on NRKW mothers. This included the number of living offspring an adult female had in a given year, whether her living offspring included at least one son (henceforth "has son"), and if her son was an adult male (henceforth "has adult son"). We also included annual chinook salmon abundance to account for how social covariates may interact with salmon abundance (see chapter 1 for methods on salmon abundance estimates).

2.0 Statistical modelling

Using the programming software R 4.2.3 (R Development Core team, 2023), we conducted statistical analysis to investigate how the body condition of NRKW adult females might be associated with demands due to provisioning offspring (while accounting for salmon). We constructed a set of six candidate models on only adult females (age 12 or greater, n = 229) based on *a priori* hypotheses (Supplementary Table 4). We then fit the data with linear mixed effects models and a Gaussian distribution using the R package glmmTMB (Brookes *et al.*, 2017).

To evaluate which characteristics of adult females and their offspring were associated with body condition, we competed models including individual level covariates and covariates relating to a whale's offspring. Offspring covariates included the number of offspring an adult female had, and whether the whale had a son. To evaluate whether the effect of a son on a mother's body condition depended on the son's age, we introduced another model considering whether an adult female had an adult son. Each model included the adult female's age, fit with a cubic natural spline (df = 3) to address non linear allometric patterns in body condition (Stewart et al., 2021). Our models included interactions between age and all offspring covariates as the relationship between offspring covariates and adult female's body condition may depend on the female's age. We also included models with a salmon and offspring covariate interaction term to address the potential influence food availability may have on maternal provisioning. Finally, we used whale identity and matriline identity as random effects to account for individual and group level variation.

We evaluated model selection using the Akaike Information Criteria (AIC; Anderson & Burnham, 2002), considering models within 2 AIC points of the top performing model (lowest AIC) as competitive, unless simpler models had lower ΔAIC (the difference in AIC between each model and the best model) than more complex models (Anderson & Burnham, 2002; Arnold, 2010). We validated model performance using the R package DHARMa (Hartig, 2022), and assessed covariate strength by evaluating coefficients and their 95% confidence intervals within our top models. We also computed relative variable importance (RVI) values for each term in our top models to understand which variables had the strongest predictive influence on body condition.

Results

We observed variation in eye patch ratio (0.99-1.26 range, n = 229 observations, 75 individuals), much of which related to individual and offspring-related covariates. Broadly, eye patch ratio increased with age, and eye patch ratio varied with reproductive status (Figure 5). After accounting for these individual level variables, we found evidence that offspring covariates were associated with body condition. Our analysis indicated that the number of offspring a female had was the most important offspring predictor of body condition (indicated by AIC and RVI values). The influence of our salmon covariate on body condition was modest; we observed a slight but negative association (Figure 5, Supplementary Figure 4), and no interaction term that included salmon was significant (Supplementary Figure 5).

Multi-model inference suggested that a simple model containing the number of offspring as the only offspring covariate was the best predictor of body condition (AICc weight = 0.64, Table 2), and was the only competitive model in the model set (See Methods). The top model explained 89% of the variation, with fixed effects explaining 19% of the variation. The number of offspring an adult female had was 12 times more important in explaining variation in eye patch ratio (RVI = 0.47) compared with whether a female had a son (RVI = 0.04). The effect of whether a mother had a son was not influenced by the age of the son (Table 2, Δ AIC = 12.63, RVI = 0.00, P = 0.82, Supplementary Table 3).

An adult female's eye patch ratio was negatively associated with the number of offspring she had (Figure 5, 6). There was no significant interaction between number of offspring and age, but there was considerable uncertainty in this relationship among younger adult females (age 17), given that whales of this age are unlikely to have more than two offspring (Figure 6). For the average age of adult females in the data set (age 28), there was a negative association between body condition and number of offspring (slope = -0.007, 95% CI: -0.014 to -0.001), with a similar pattern among older adult females (age = 40, slope = -0.010, 95% CI: -0.017 to -0.004).

Table 2. Model selection results (n = 229 observations, 75 whales). Models varied by which social covariate was included (indicated in 'social covariate' column), and whether salmon abundance was also considered in interaction terms with the social covariate (denoted by an x). For each model, the social covariate it contained was also considered in interaction terms with age and sex. See supplemental table 4 for full list of terms for each model in the model set. The top performing models and any competitive models (See Methods) are indicated in bold font. K indicates the number of terms in the model including each degree of any natural spline covariate and interactions with natural spline covariate.

Model #	Social covariate	K	AICc	Δ AICc	AICc Weight
1	**Number of offspring**	**14**	**315.99**	**0.00**	**0.64**
2	Number of offspring x salmon	15	317.29	1.30	0.33
4	Has son x salmon	20	323.22	7.23	0.02
3	Has son	18	326.26	10.27	0.00
5	Has adult son	18	328.62	12.63	0.00
6	Has adult son x salmon	20	328.84	12.85	0.00
Null	None	4	377.60	61.61	0.00

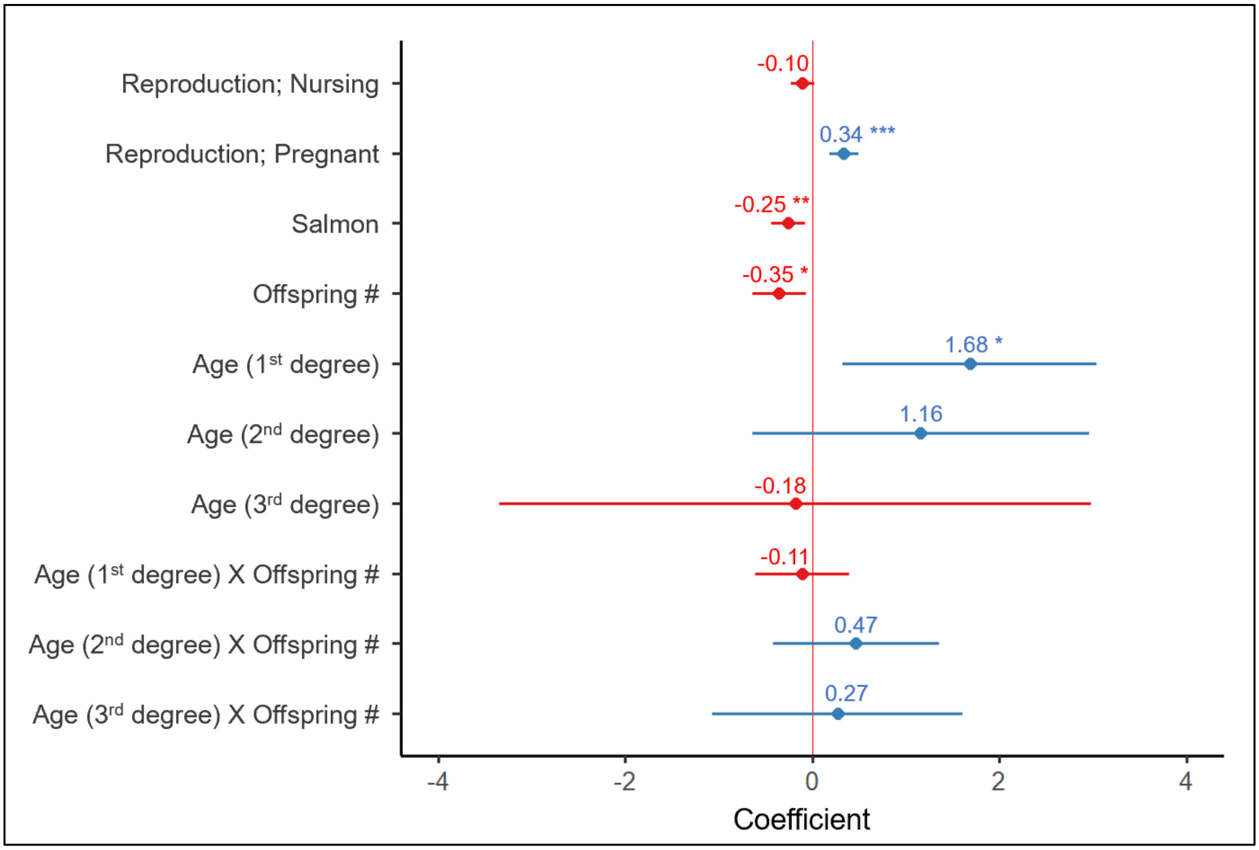


Figure 5. Coefficients (dots) and 95% confidence intervals (lines) for fixed effects in the top performing model (model #1) for predicting eye patch ratio among all adult females. Symbols denote P values (*** = 0.0001, ** = 0.001, * = 0.01, · = 0.05). Blue values indicate positive associations and red values indicated negative associations between predictors and eye patch ratios. Categories denoted by ';' represent level of the predictor variable compared to the base case level. Brackets around age terms represent the degree of natural spline function for age.

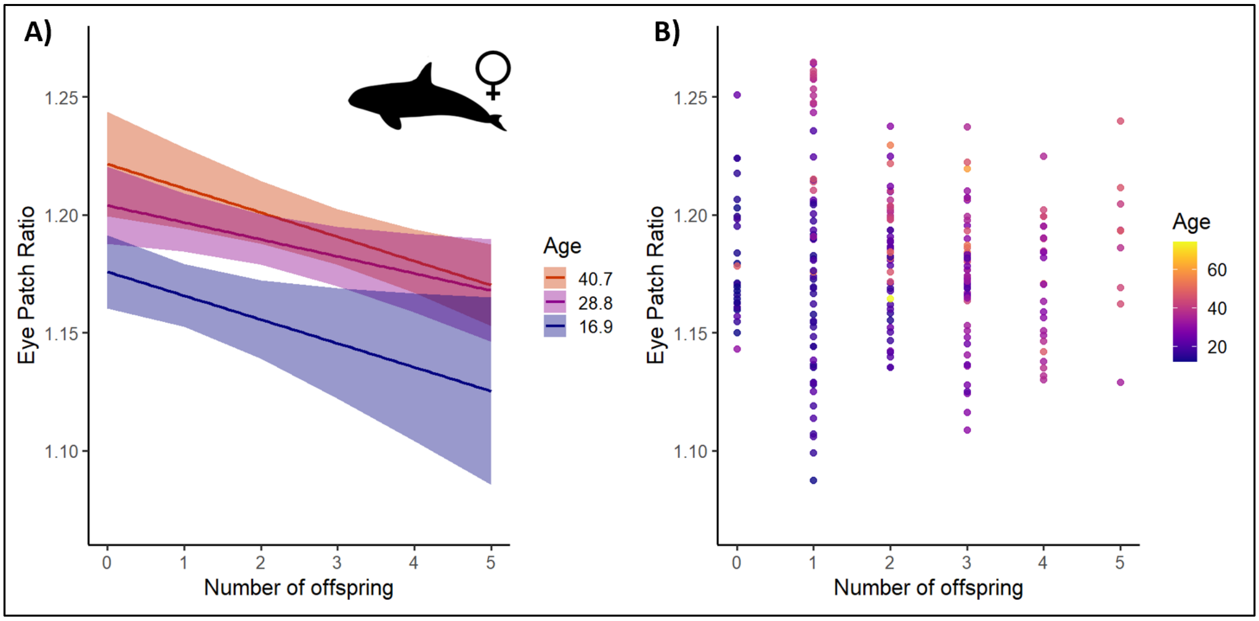


Figure 6. Top performing model (model #1) predicting body condition of adult females. A) Predicted eye patch ratio values by age as a function of the number of offspring and adult female had. All other model terms are held constant at their mean. Age is represented visually as three categories: the mean age of adult females in the data set (28.8), mean age plus one standard deviation (40.7), and mean age minus one standard deviation (16.9). Lines represent model predicted values and shaded areas represent 95% confidence intervals. B) Raw data showing range of adult female eye patch ratio values in association with number of offspring a female has, according to age.

Discussion

Our analysis showed that NRKW mothers incur physiological costs from investing in their nondispersing offspring. Specifically, an adult female's body condition was negatively associated with the number of offspring, regardless of her age. Contrary to our predictions, offspring sex did not influence a mother's condition. Additionally, neither these patterns nor female body condition were influenced by chinook salmon abundance, suggesting that social factors are important regardless of prey abundance during the time of this study. Our results suggest that nondispersal and continual provisioning of offspring may limit a mother's ability to provision herself, and these physiological costs might impose further costs to maternal fitness and population dynamics by limiting future reproduction.

1.0 Limitations

While our analysis found significant patterns in the body condition of NRKW adult females, several limitations should be considered in interpretation. Our sample size was modest, with multiyear samples from 75 individuals. This dataset, however, represented approximately 60% of the populations' reproductive females in 2024 (Alert Bay Cetological Society, 2022). Furthermore, our ability to detect a relationship between body condition and salmon abundance (or any interactions with offspring covariates) may have been limited by our measure of chinook salmon abundance (see Chapter 1 for further discussion). More broadly, our analysis cannot definitively link lower body condition to costs of provisioning offspring. For example, lower body condition in adult females could also result from reduced or ineffective foraging, not solely from provisioning offspring. For example females capture less prey if they have a calf (Tennessen et al., 2023) and the presence of many young offspring might reduce foraging and therefore body condition. We reason, however, that this explanation alone is unlikely, given the high dependency of offspring on provisioning (Wright et al., 2016), and lack of evidence that group size limits a female's foraging ability (See Chapter 1). Additionally, the cumulative effect of multiple pregnancies and lactation periods over a female's lifetime could negatively influence her body condition. Future studies could investigate whether lower condition in mothers represents the effects of costs from post-lactational care of offspring or simply reproductive costs alone.

2.0 Adult female body condition depends on offspring number but not offspring sex

With these limitations in mind, our results suggest that NRKW females with more offspring consume less prey due to higher parental care demands. Similar patterns are described in semelparous spiders (*Stegodyphus lineatus*), where mothers show a smaller decrease in body condition when provisioning experimentally reduced broods (Salomon et al., 2005). Lower condition in NRKW mothers with more offspring highlights the potential cost of nondispersal and lifelong parental care, especially as mothers are challenged by provisioning their adult male offspring in addition to younger offspring. While nondispersal in RKWs may offer social benefits such as alloparental care, kin-directed prey sharing, and intergenerational learning (Waite, 1988; Brent et al., 2015; Wright et al., 2016), we demonstrate that it can also impose physiological costs for mothers. Cooperation from other mature matriline members could alleviate these costs and improve offspring provisioning, as observed in meerkats (*Suricata suricatta*) and African hunting dogs (*Lycaon pictus*) (Clutton-Brock et al., 2004; Marneweck et al., 2019; Jordan et al., 2023). Sharing in NRKWs is not limited to mother and offspring; post reproductive females share prey with other adult females and increase the probability of survival of their grandoffspring (Wright et al., 2016; Nattrass et al., 2019), suggesting cooperative provisioning could reduce costs from parental care. Moreover, adult males sometimes babysit their younger siblings while mothers forage (Waite, 1988). These processes, however, do not to seem to buffer declines in adult female body condition in association with provisioning their multiple offspring.

Contrary to our expectations, adult females with sons did not have lower body condition than those with only daughters. This result is surprising, given that caring for sons can reduce the future reproductive output of Southern Resident killer whale (SRKW) females (Weiss et al., 2023). Potentially, costs of rearing sons might only be reflected in a mother’s future reproductive output rather than in a mother’s body condition, as seen in big horn sheep (Berube et al., 1996).

Alternatively, NRKWs comprise a growing population compared to the endangered SRKWs (Vélez-Espino et al., 2014); suggesting that stressors facing the NRKWs are lower and mothers are able to raise energetically demanding sons with fewer consequences to their fitness. Foraging and prey sharing dynamics of NRKW males may also differ from SRKWs, given that foraging capture rates of each age-sex class differ between the two populations (Tennessen et al., 2023). However, NRKW males appear to be more dependent on maternal provisioning, spend less time foraging than SRKW males, and have a lower prey capture rate (Tennessen et al., 2023), suggesting that NRKW males may in fact be more costly. This pattern aligns with the recent evidence that immature and teenage males might receive less provisioning when their matriline has more dependent juveniles to provision (Chapter 1). Therefore, the costs of increased care requirements might be reflected in a son's body condition rather than a mother's body condition if mothers divert investment from costly sons to meet the demands of additional offspring.

3.0 Future research and implications

Our study highlights the costs associated with lifelong provisioning of offspring, but further research is needed to understand how these observed physiological costs might influence the survival of offspring and parents. While our findings suggest that adult females provide less for themselves or expend more energy as they have more offspring, it is unclear if their offspring also receive reduced provisioning as their number of siblings increases. Larger broods can promote sibling competition (Godfray & Parker, 1992; Neuenschwander et al., 2003), and examining how the number and sex of siblings influence a whale's body condition could reveal if offspring with more siblings receive less maternal provisioning. Examining costs of sibling competition could also help decipher if mothers reduce offspring provisioning when they have more offspring to feed (as suggested in Chapter 1), or if they continue to provision their offspring at their own expense and the expense of future reproductive opportunities (Weiss et al. 2023). Additionally, it remains unclear if the physiological costs demonstrated here impact survival or future reproductive output in NRKWs. Given body condition estimates from eye patch ratios are associated with survivorship in RKWs (Stewart et al., 2021), it is likely that the number of offspring could influence survival in mothers. That being said, yearly survival rates in NRKW adult females high (0.88-0.99; Vélez-Espino et al., 2014), suggesting that the cost of parental care to mothers is unlikely affect survival.

Our work illustrates the importance of considering the health of breeding individuals in the conservation of at-risk species and offers insights on parental investment in a system with unusual nondispersal of both sexes. Uncertainty remains around whether our measure of salmon abundance accurately reflects prey availability for NRKWs. However, our study shows that NRKW females face intrinsic costs from provisioning their offspring throughout their lives, even if limited prey does not exacerbate these costs. Furthermore, our results indicate that, although female RKW can produce a new calf approximately every three years (Olesiuk et al., 2005), the costs of maintaining multiple offspring maylimit lifetime reproductive output. Conservation management should consider these inherent challenges faced by NRKWs, given that environmental changes including increased noise pollution, containments, and reduced prey availability could cumulatively burden reproductively valuable members of this threatened population (Clarke Murray et al., 2019). Importantly, investigating the physiological costs of parental care in the Endangered SRKWs should be examined given that their population is declining and face greater environmental and genetic stressors compared to NRKWs. Since SRKW body condition and survival are influenced by current salmon abundance (Stewart et al., 2020), contrary to our finding on NRKW body condition, we could expect similar recovery prospects for SRKWs if their prey availability was in alignment with conditions experienced by NRKWs. More broadly, our study shows that mothers incur costs from nondispersal of male and female offspring, facing challenges in provisioning offspring of different ages and cumulative costs from the simultaneous care of multiple offspring. Finally, applying well-studied behavioural concepts like parental investment to social systems with extreme sociality can reveal the complexity and variety of reproductive behaviour and life history strategies.

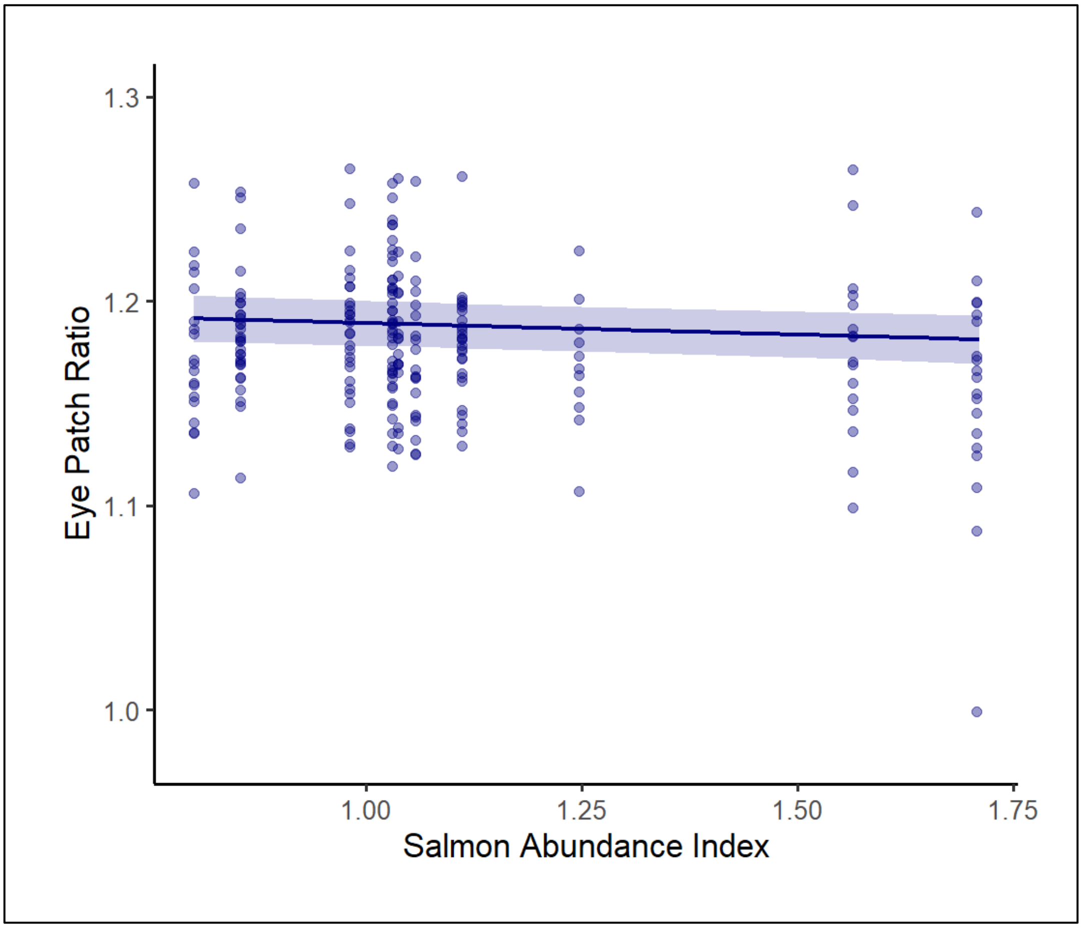
Supplementary Material: Chapter 2

Supplementary Table 3. Relative Variance Importance factor (RVI) of social covariates and associated interaction terms (adult females only, n = 229). Individual level covariates such as age and reproductive status, as well as salmon abundance are not shown because these terms were included in every model and thus their associated RVI is uninformative

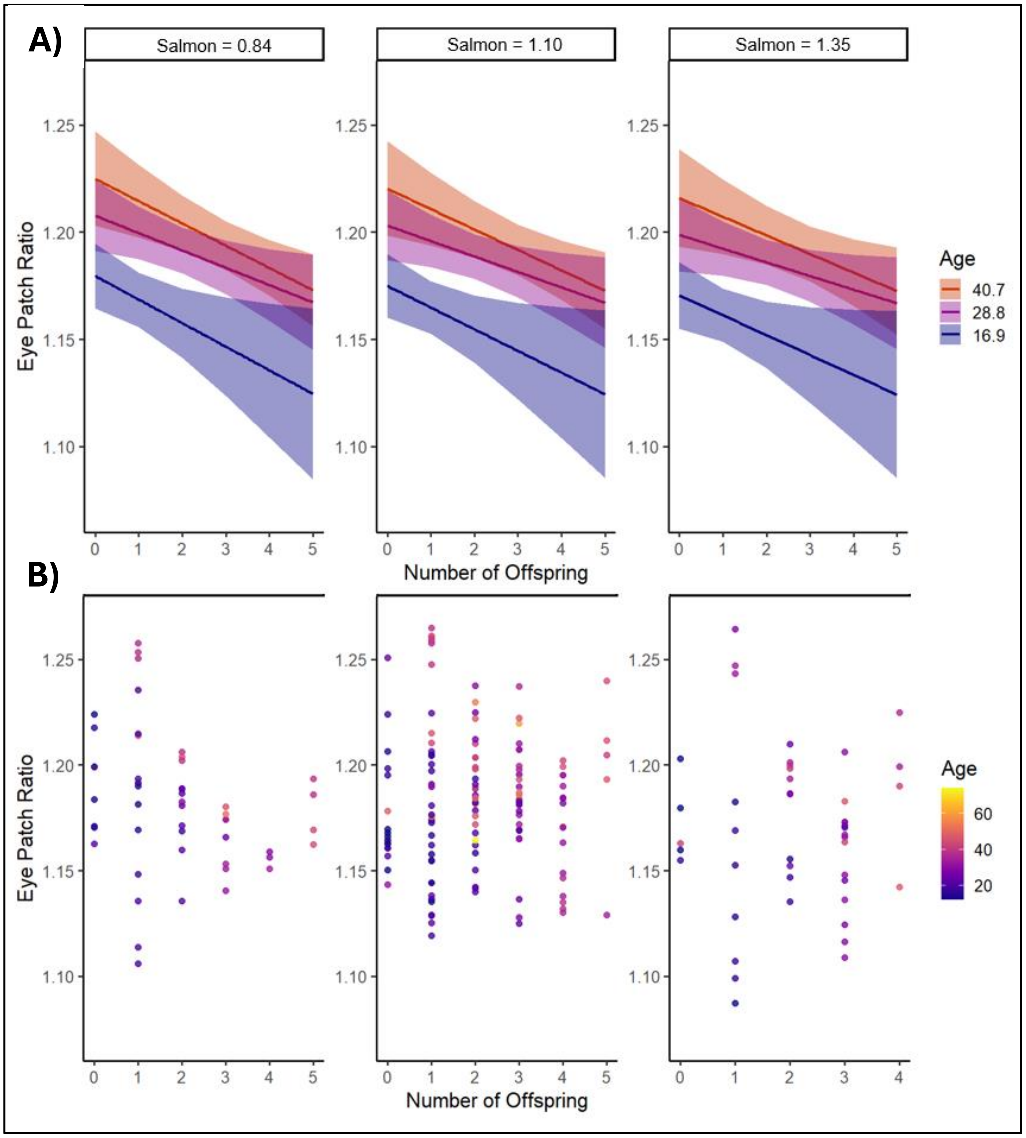
Predictor Variable	**RVI**
Number of offspring	0.47
Age X number of offspring	0.47
Salmon X number of offspring	0.35
Salmon X Has son	0.04
Has son	0.03
Age X Has son	0.03
Salmon X Has adult son	0.00
Has adult son	0.00
Age X has adult son	0.00

Supplementary Table 4. List of candidate models for analysis on adult female body condition (n = 229). Models 1-6 include random effects of whale ID and matriline ID

Null Model	
Null	1 + random effects (whale ID and matriline ID)
Number of offspring models	
1	Number of offspring x age + salmon + reproductive status + age
2	Number of offspring x age + number of offspring x salmon + salmon + reproductive status + age
Has son models	
3	Has son x age + salmon + reproductive status + age
4	Has son x age + has son x salmon + salmon + reproductive status + age
Has adult son models	
5	Has adult son x age + salmon + reproductive status + age
6	Has adult son x age + has son x salmon + salmon + reproductive status + age



Supplementary Figure 4. Effect of salmon abundance on predicted eye patch ratio from top model. All other model terms are held constant at their mean. Blue line and shaded blue area indicate model predicted eye



Supplementary Figure 5. Second ranking model (Δ AIC = 1.30) from model set revealing the effect of number of offspring and salmon interaction term. A) Top panels indicate model predicted eye patch ratio values by age and salmon abundance as a function of number of offspring. Salmon abundance is represented visually as three categories (the mean abundance (1.10), mean abundance plus one standard deviation (1.35), and mean abundance minus one standard deviation (0.84). All other model terms are held constant at their mean. Lines represent model predicted values and shaded areas represent 95% confidence intervals. B) Bottom panels indicate raw data showing range of eye patch ratio values for adult female NRKWs in association with number of offspring, according to age and salmon abundance. Salmon abundance is categorized into three groupings according to mean abundance +/- one standard deviation.

Conclusion

What has studying the sociobiology of RKWs taught us about how animals manage intragroup conflict and allocate resources and parental investment? Research on these topics has spanned decades and expanded from early studies on bird clutch size to more recent work on a variety of mammals (Clutton-Brock, 1991; Godfray & Parker, 1992; Hudson & Trillmich, 2008; Geary, 2015). However, to our knowledge, much of our understanding is limited to species where offspring eventually disperse and parental care is relatively short-term. Our work on RKWs generates questions around how conflict over parental investment and resource allocation occurs in highly social systems that often mirror our own.

Sharing resources with close relatives over a lifetime poses unique challenges compared to systems where kin eventually disperse. Conflict between kin can result in fitness costs even to winners, as their inclusive fitness is tied to the survival of their rival kin (Hamilton, 1964). In African wild dogs (*Lycaon pictus*), packs are kin-based, and aggression is rare, occurring only among unrelated males (Jordan et al., 2023). Similarly, aggressive displays and overt physical competition over shared prey are not documented in RKWs (Ford & Ellis, 2006; Wright et al., 2016) despite evidence for aggression among conspecifics (Robeck et al., 2019; Grimes et al., 2022). Potentially, in systems with nondispersing kin, conflict may be limited to providers and recipients rather than between competing recipients. This conflict might take a passive form through diminished investment via shared prey rather than direct aggression.

In many social species, intragroup conflict is mitigated through fission-fusion dynamics, where groups disperse and rejoin based on environmental or social conditions. For example, African lions (*Panthera leo*), adjust their social group size according to savanna productivity (Palmer et al., 2023). RKWs also exhibit social group splitting in response to lower food availability and changes in matriline demographics (Stredulinsky et al., 2021). However, emigration of natal family members is rare (Bigg et al., 1990) and the probability of matrilines reuniting is low (Stredulinksy et al., 2021). This pattern is similar to African elephants (*Loxodonta* Africana), where higher tier social groups split but natal group stability is maintained during resource limitations (Wittemyer et al., 2005). Perhaps for societies with nondispersing kin, reduced provisioning of recipients or increased cooperation could mitigate intragroup competition when resources are scarce, in lieu of dispersal.

Set hierarchies can also mitigate conflict in social groups, but to our knowledge, such a system is not apparent in RKWs. Species with high social stability often distribute resources based on hierarchies (Tilson & Hamilton, 1984; Gese et al., 1996; Smith & Holekamp, 2023), including ranking among non-kin members (Clutton-Brock et al., 1998). Due to the nondispersal of kin in RKWs, hierarchy might be based on relatedness, with provisioners holding power over shared resources and favouring close relatives (Wright et al., 2016) or those with the highest reproductive value. African lions (*Panthera leo*) do not allocate resources by dominance hierarchies, even in male groups where individuals less related (Palmer et al., 2023). However, Asiatic lions (*Panthera leo persica*) (Chakrabarti et al., 2023) which have access to smaller prey, do have hierarchies for sharing prey among male groups. In RKWs, if hierarchies are established by sharing prey with close relatives, an abundance of prey might weaken these hierarchies and promote sharing with non-kin.

Finally, other species also exhibit nondispersal of both sexes (Amos et al., 1993; Park et al., 1998; Rodrigues et al., 2010) and investigating conflict and resource allocation in these social systems could reveal similar patterns. Do these systems also show that young males receive less provisioning under more challenging social group composition, while provisioning of females is maintained? Are older males provisioned despite their high caloric requirements, or are they better independent foragers? Are the costs of bearing and continuously caring for multiple philopatric offspring reflected in other systems or does cooperation from more mature offspring help alleviate these costs? Exploring these complex behaviours in social systems often akin to our own can further our understanding and appreciation of how animals live together.

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