Allocation of parental care by Western Canada Geese *Branta canadensis moffitti*

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Abstract

The level of parental care provided by Western Canada Geese *Branta canadensis moffitti* to their goslings (4–11 months of age) was measured in a resident population by determining proximity of goslings to the nearest parent, goslings' daily attendance in the family unit, and the duration of the parent-gosling association during the first winter. Time spent in vigilance postures (watching for competitors and predators) and aggression (to maintain space for foraging within flocks) was determined for each family member. Male goslings were more "helpful" in that they were more vigilant and aggressive than female goslings. Perhaps as a result, male goslings benefited more from all three measures of parental care than female goslings. Male goslings were on average closer to parents, in attendance more often, and had a longer duration of parent-gosling association during the first winter than their female siblings. Among females in the same brood (*i.e.* siblings), the most vigilant and aggressive were allocated more care as measured by proximity to parents, daily attendance, and duration of association with parents. Among male siblings, the most vigilant individuals were allocated with more care in terms of proximity to parents than less vigilant male goslings. Within sexes, gosling structural size (*i.e.* skull length) did not affect the allocation of parental care. With regard to parents, the level of female vigilance and aggression towards flock members was negatively correlated with the amount of "help" provided by the most "helpful" gosling in the brood, in terms of the goslings' contribution to the family through their vigilance and aggressive behaviours. This finding suggests that female parents benefit from maintaining contact with "helpful" goslings, more so than females with less "helpful" goslings. This relationship was not apparent for male parents. The most interesting finding from this study was that parent geese appeared to base parental investment decisions more on their goslings' behaviour rather than structural size. The energetic costs that mature goslings bear from assisting parents with family duties of watching for competitors and predators and defending foraging space within flocks may be compensated by longer-term benefits of prolonged association with their parents.

Key words: aggression, brood, Canada Geese, family, goslings, offspring, parental care, social, vigilance.

The mating system of wild geese and swans is characterised by: (1) long-term pair bonds, (2) biparental care, and (3) extended parent-offspring association (Kear 1970). In winter, goose and swan flocks typically consist of a combination of families, paired birds, and single subadults or adults prospecting for a mate (Boyd 1953; Evans 1979; Owen 1980; Scott 1980a). Family units include the parental pair and their offspring from the previous summer (Boyd 1953; Raveling 1970). Parents spend much of their day being vigilant to the threat of competitors or predators, and on defending space within the flock to enable disturbance-free foraging for their offspring (*i.e.* parental care: Scott 1980b,c; Black & Owen 1989a,b). The extra time that parents spend on vigilance and aggressive behaviour takes away from other essential daily activities, and for several species in the Anserinea subfamily has been used as a quantifiable measurement of parental investment in their young (Lazarus & Inglis 1978; Scott 1980b; Akesson & Raveling 1982; Black & Owen 1989a).

The timing of family break up in geese varies within and among species (Owen 1980), ranging from less than a full year for Cackling Geese *Branta hutchinsii minima* (Johnson & Raveling 1988) to remaining with parents over several winters for Greenland White-fronted Geese *Anser albifrons flavirostris* (Warren *et al.* 1993). In Barnacle Geese *Branta leucopsis*, most parents are seen with goslings in the first month after return to the wintering grounds (*i.e.* when the goslings were 4 months old), to a lesser degree during early winter (age 5–9 months), and even fewer parents continue to associate with their goslings in spring and during the return migration (10–11 months; Black & Owen 1989a). Barnacle Goose parents threaten and peck their offspring with increasing regularity during mid–late winter, suggesting that some (but not all) goslings leave the family because of this harassment (Black & Owen 1989a). As families become smaller, parental effort in vigilance and defence of foraging space eventually declines as mature goslings increase their participation in these behaviours (Black & Owen 1989a,b). This observation led to the suggestion that gosling "help" may enable parents to acquire essential body stores for the coming breeding season (Black & Owen 1989a). Furthermore, parents that maintained their association with at least one gosling for the longest period into the spring, bred more successfully in the following summer compared to those with shorter associations with goslings (Black & Owen 1989a). These observations lead to the question of how parents decide which goslings to expel and which to keep in the family. For example, do parents favour more "helpful" offspring?

Considering the parent-offspring relationship from the perspective of offspring in goose flocks, goslings may benefit from continued association with parents by increased social status and gaining access to prime feeding sites compared to goslings that curtail association with parents (Raveling 1970; Black & Owen 1984, 1987, 1989a,b; Sirwardina & Black 1999; Raveling *et al.* 2000). These benefits are similar to those described for Bewick's Swan *Cygnus columbianus bewickii* families, where cygnets in closest proximity to parents fed more, were threatened less by neighbours, and were more successful in aggressive encounters than individuals farther from parents (Scott 1980b). In Barnacle Geese, males that bred at least once during their lifetime spent significantly longer periods with their parents during their first winter than males that did not breed; there was no such difference for females (Black *et al.* 2014). These observations led us to question whether different goslings are allocated more than their share of the benefits of parental care (*i.e.* sibling rivalry, *sensu* Mock & Parker 1997). Theoretical arguments suggest that under variable environmental and ecological conditions, parents may extend unequal care to individual offspring (Winkler 1987; Clutton-Brock 1991), and that parents are expected to invest more in offspring with characteristics that result in higher inclusive fitness (Trivers 1972). For example, in some systems it might pay parents to invest more in the smallest, or weakest offspring in greatest need (Lessells 2002).

Assuming that young geese and swans gain substantial benefits from their association with parents, researchers have measured the allocation of parental care in terms of nearness or proximity to parents, daily attendance in the family, and the duration of the parent-offspring association during the first year (Scott 1980b; Black & Owen 1989a; Black *et al.* 2014). The aim of this paper is to contribute to understanding how parental care is allocated within goose families. Using Western Canada Goose *Branta canadensis moffitti* broods as our model system, we examined whether parents provided more care to more "helpful" offspring or whether the amount of care was distributed in relation to goslings' relative "need". To this end, we tested whether the characteristics of individual offspring (*e.g.* sex, behaviour, and structural size) influenced allocation of parental care (*sensu* Clutton-Brock *et al.* 1981; Stamps *et al.* 1985). We also determined whether parents experienced any noticeable benefit from maintaining contact with "helpful" goslings by quantifying the change in parental effort devoted to maintaining space around family members (*sensu* Black & Owen 1989a).

Methods

This study was conducted on the pastures and saltmarshes adjacent to Humboldt Bay (40°47'44"N, 124°7'7"W) in northwest California, USA. The Arcata Bottomlands to the north of Humboldt Bay is comprised primarily of pastures managed for dairy cattle, sheep and cattle. The Humboldt Bay National Wildlife Refuge (HBNWR) to the south contains permanent and seasonal wetlands, saltmarsh and hay fields.

The study population of about 1,500 Western Canada Geese used these habitats during winter, breeding and brood-rearing (Griggs & Black 2004). In June 2000, 97 adult geese and 192 goslings were captured while flightless using a corral trap (*sensu* Cooch 1953). Birds were aged, sexed through cloacal examination, fitted with a U.S. Fish and Wildlife Service metal leg-ring and an alpha-coded plastic neck-collar, then weighed and measured (skull length; Dzubin & Cooch 1992). Most goslings hatched in April 2000, although exact hatch dates were not determined.

From 1 July 2000, after most goslings had fledged and parents completed their wing moult, through to the end of March 2001, flocks with collared individuals were observed with a spotting scope (Leica® 20–60×) to determine the identity of individuals within families. Average monthly flock sizes during winter ranged from 30–156 birds, peaking in November (Griggs & Black 2004). Family membership was based on the proximity of individuals, similar travel paths, mutual social displays, coordination of vigilance routines and assistance in aggressive encounters (Akesson & Raveling 1982; Black *et al.* 1996). Observations were conducted 3–5 times per week between 08:00–12:00 h (96% of dataset) and 13:00–15:00 h (4%) using a vehicle as a blind along farm roads within the study area. The average size of Western Canada Goose families on Humboldt Bay was 4.2 goslings (*s.e.* ± 0.7, *n* =35), including one family with a single gosling and one large family with 22 goslings (*i.e.* brood amalgamation). The following assessment was based on 24 families that were regularly observed (see below) with 2–10 goslings assumed to be "natural" family members (*i.e.* not adopted). Parents and goslings eventually separated when parents established nesting territories and goslings joined non-breeding flocks. Goslings were considered to be no longer associating with their parents when they were observed in a flock which did not include their parents on at least two occasions. Dates were assigned to three seasons: autumn (1 August–22 October 2000), early winter (23 October–31 December 2000), and late winter (1 January–15 March 2001).

Focal animal sampling was used to record the behavioural activity budget of parents and goslings (Martin & Bateson 1993), but our analysis in this paper focused on vigilance and aggression. At 30 s intervals, during 10 min sampling periods, the behaviour of each family member was recorded as vigilant (head and neck at an angle of > 45°) or as other daily activities. These data were converted to the proportion of intervals in vigilant posture for each bird, which was then averaged for each seasonal period (autumn, early winter and late winter). Behaviour sampling (continuous recording of conspicuous behaviours; Martin & Bateson 1993) was used to record the occurrence of initiating aggressive encounters for each family member during the entire period of observation; the initiator of aggressive encounters usually won the encounter (Boyd 1953; Black & Owen 1987, 1989b).

As goslings matured, three measures were used to describe the level of allocated parental care: (1) proximity of each gosling to nearest parent, (2) attendance (presence/absence) of each gosling in the family group, and (3) length of association with parents. These measures were based on the assumption that benefits of protection and learning opportunities were acquired when goslings were associating with their parents (*sensu* Lazarus & Inglis 1978; Raveling 1970, 1981; Scott 1980b; Black & Owen 1984, 1989a, b). The proximity of each gosling to each parent was recorded in goose-lengths (~90 cm, Bellrose 1980) at the beginning and end of each 10 min observation and averaged. This assessment was practised using goose decoys separated by different distances and angles prior to fieldwork in order to ensure accurate measures. Attendance in the family group was recorded as the proportion of days in which each gosling was seen to be associating with parents in the same flock up to the time that it was found to have left the family. The duration of parent-gosling association during the first year was calculated as the number of days from 1 August 2000 to the mid-point between date on which parents were last observed with a particular gosling and the first record without that gosling (Black & Owen 1989a).

In all analyses, indices of parental care were assessed in terms of proximity to parents, gosling attendance in the family, and the duration of the parent-offspring bond prior to family break-up. Indices of gosling "help" included their contribution to maintaining family status and position in flocks (*i.e.* goslings' vigilance and aggressiveness). For an index of goslings' relative "need" (see page 46), we used a measure of structural size (*i.e.* skull length). Sexes were analysed separately because male geese were generally larger, more vigilant and aggressive than females (Akesson & Raveling 1982; Black & Owen 1987, 1989a,b). All comparisons were conducted among siblings within broods. This removed the need to control for gosling age among broods and reduced bias due to parent quality. After testing and confirming normality and equal variance in the three measures of parental care (proximity to parents, gosling attendance, family duration) we use ANOVA to test for variation in these measures over the three times of year (autumn, early winter and late winter).

To determine whether the amount of parental care (*i.e.* proximity to parents, attendance in the family, and duration with parents) was attributed unequally among goslings, we created two gosling categories from among siblings of the same sex. Category I (highest care) was assigned to the individual of each sex that received the very highest level of care in each brood. Category II (low care) was assigned to siblings of the same sex that received substantially less parental care – *i.e.* more than half a standard deviation less than the average value for all siblings of that sex in the brood. Families were not included in this analysis if these criteria were not met, thus reducing the sample of 24 families to *e.g.* 10, 7 and 5 families for the analysis of proximity to parents, attendance in the family and duration with parents, respectively, for comparison among female siblings. We used mean values for goslings' attributes (behaviour and size, see below) when multiple siblings of the same sex were included in Category II. Non-parametric Wilcoxon signed-rank tests were used to test for differences between Category I (highest care) and Category II (low care) in terms of the goslings' "helpful" behaviours (*i.e.* proportion vigilant and rate of aggression) and structural size (*i.e.* skull length).

Kruskal-Wallis tests were used to assess variation across the three season categories (autumn, early winter, late winter) in proportion of time spent performing different behaviours (*i.e.* proportion vigilant and rate of aggression).

To determine whether parents appeared to reduce their effort in terms of vigilance and aggression in relation to gosling "help" with these behaviours, we used Spearman Rank Correlation tests of parents' and goslings' behaviours. For this analysis, we calculated the change in parents' vigilance and aggression from early winter to late winter. For goslings, we calculated mean vigilance and rate of aggression from observations taken during early and late winter periods, and used values from the single most "helpful" gosling in each brood (*i.e.* the highest level of vigilance and aggression). Using these criteria reduced the sample of 24 families to 14 and 17, respectively, for the tests of vigilance and aggression.

Results

Western Canada Goose families were resighted and behaviours recorded 9–24 times during the course of the study (mean ± s.e. = 18.8 ± 0.9 resightings per family). To assess whether the parent-offspring associations changed over time, we compared goslings' average proximity to their parents and also family attendance in autumn, early winter and late winter. Gosling proximity to parents was greatest (ANOVA, males: $F_{2,123} = 3.49$, $P = 0.03$; females: $F_{2,115} = 11.78$, $P < 0.001$), and family attendance was lowest (males: $F_{2,124} = 32.46$, $P < 0.001$; females: $F_{2,116} = 62.0$, $P < 0.001$) in the late winter period (Fig. 1). Parent geese established nest sites and territories on levies and islands in the Humboldt Bay area soon after this late winter period (Griggs & Black 2004), which is when the 10–11 month old goslings were observed in flocks in adjacent pastures without their parents.

To assess whether goslings increased their contribution towards maintaining foraging space within flocks, we compared goslings' behaviour across different times of year when goslings and parents were still together in families. The proportion of time that goslings spent being vigilant was greatest in late winter (Kruskal-Wallis, males: $H_2 = 10.73$, $P = 0.005$; females: $H_2 = 9.30$, $P = 0.01$) (Fig. 2). Levels of aggression (measured as frequency/h) were greatest among male goslings in early winter ($H_2 = 15.9$, $P < 0.001$); although female goslings followed a similar trend, the difference between the three time periods was not significant ($H_2 = 2.15$, n.s.; Fig. 2).

There was no significant difference in vigilance behaviour among different times of year in male or female parents. Aggression levels were greatest in early winter in adult females ($H_2 = 7.78$, $P = 0.02$), but did not differ significantly across time periods for adult males.

On comparing the association between male and female siblings with their parents, male goslings were found to be in closer proximity to their parents, had higher levels of attendance in the family, and had a longer length of association with parents than their female siblings (Table 1). This suggests that males received more of the benefits than their female siblings from the parent-offspring association. Males were also

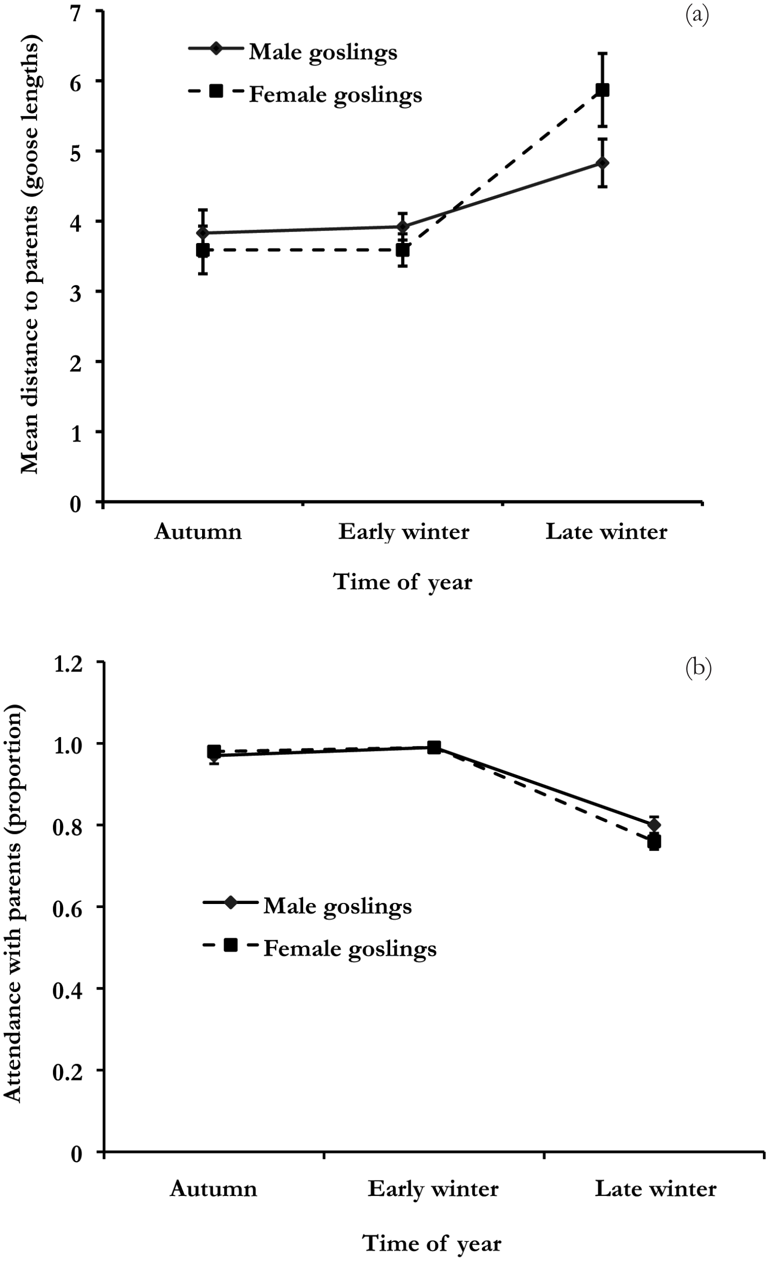

Figure 1. (a) Average distance from parents in goose lengths, and (b) attendance with parents (proportion of resightings where associating with parents), recorded for male and female Western Canada goose goslings during three time periods. Error bars are +/– one standard error.

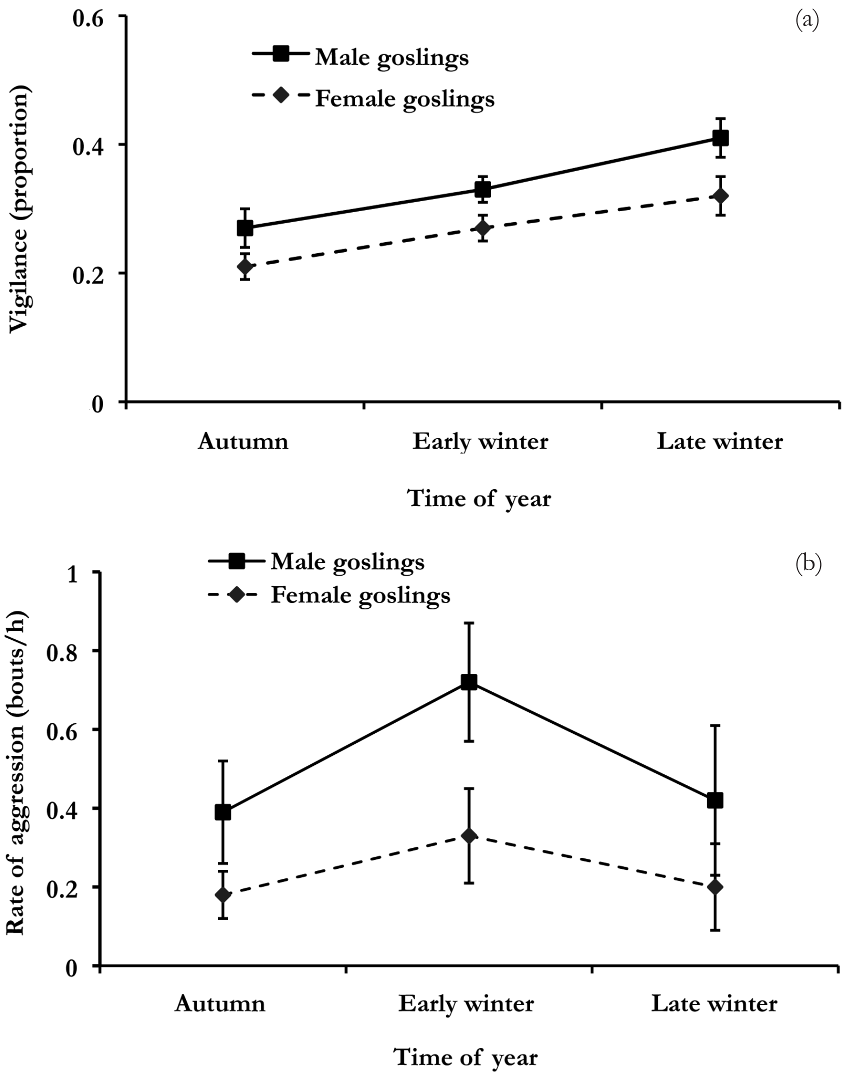

Figure 2. (a) Average proportion of time vigilant and (b) rates of aggression toward flock members in male and female Western Canada Goose goslings during 3 periods throughout the non-breeding season. Error bars are +/– one standard error.

significantly larger, more vigilant and more aggressive than female siblings (Table 2).

Within-sex comparisons among siblings indicated that parents may have allocated care based on behavioural rather than structural size. For example, Category I females (classed as having the highest level of parental care) were significantly more vigilant than Category II (low care) females (Wilcoxon signed-rank tests for each of the

Table 1. Levels of parental care provided to male and female goslings within broods of Western Canada Geese at Humboldt Bay, California from August 2000–March 2001. [a]*Z* and *P* values are the results of Wilcoxon signed-rank tests for differences in parental care accorded to male and female goslings. [b]Proximity = goslings' average distance to parents (in goose-lengths). [c]Attendance = gosling attendance with parents (proportion of resightings). [d]Duration = gosling duration with parents (in days from 1 August).

	Male			Female				
	Mean	**s.e.**	***n***	**Mean**	**s.e**	***n***	***Z*[a]**	***P***
Proximity[b]	4.36	0.43	18	5.38	0.62	18	2.20	0.027
Attendance[c]	0.80	0.49	11	0.69	0.05	11	2.31	0.021
Duration (days)[d]	216.3	5.23	7	200.3	5.08	7	2.20	0.028

Table 2. Differences in the behavioural and physical characteristics of male and female goslings within broods of Western Canada Geese in the Humboldt Bay Area, August 2000–March 2001. Measures of aggression were toward individuals outside of family. *Z* and *P* values are the results of Wilcoxon signed-rank tests for differences between the sexes for each measure.

	Male			Female				
	Mean	**s.e.**	***n***	**Mean**	**s.e.**	***n***	***Z***	***P***
Proportion time vigilant	0.33	0.02	18	0.29	0.02	18	2.11	0.035
Rate of aggression (bouts/h)	0.64	0.14	18	0.4	0.09	18	2.35	0.019
Skull length (mm)	109.8	1.16	18	107.5	1.38	18	2.24	0.025

three measures of parental care: proximity $Z = 2.80$, $n = 10$, $P = 0.005$; attendance $Z = 2.37$, $n = 7$, $P < 0.02$; duration $Z = 2.02$, $n = 5$, $P < 0.05$; Fig. 3). Category I (highest care) females were also more aggressive than Category II (low care) females (proximity $Z = 2.39$, $n = 10$, $P < 0.02$; attendance $Z = 1.96$, $n = 7$, $P = 0.05$; duration $Z = 2.03$, $n = 5$, $P < 0.05$) (Fig. 3). This trend was similar on comparing vigilance levels for Category I and II males, but only one of the three measures of parental care was statistically significant (proximity to parents: $Z = 2.34$, $n = 20$, $P < 0.02$). Category I

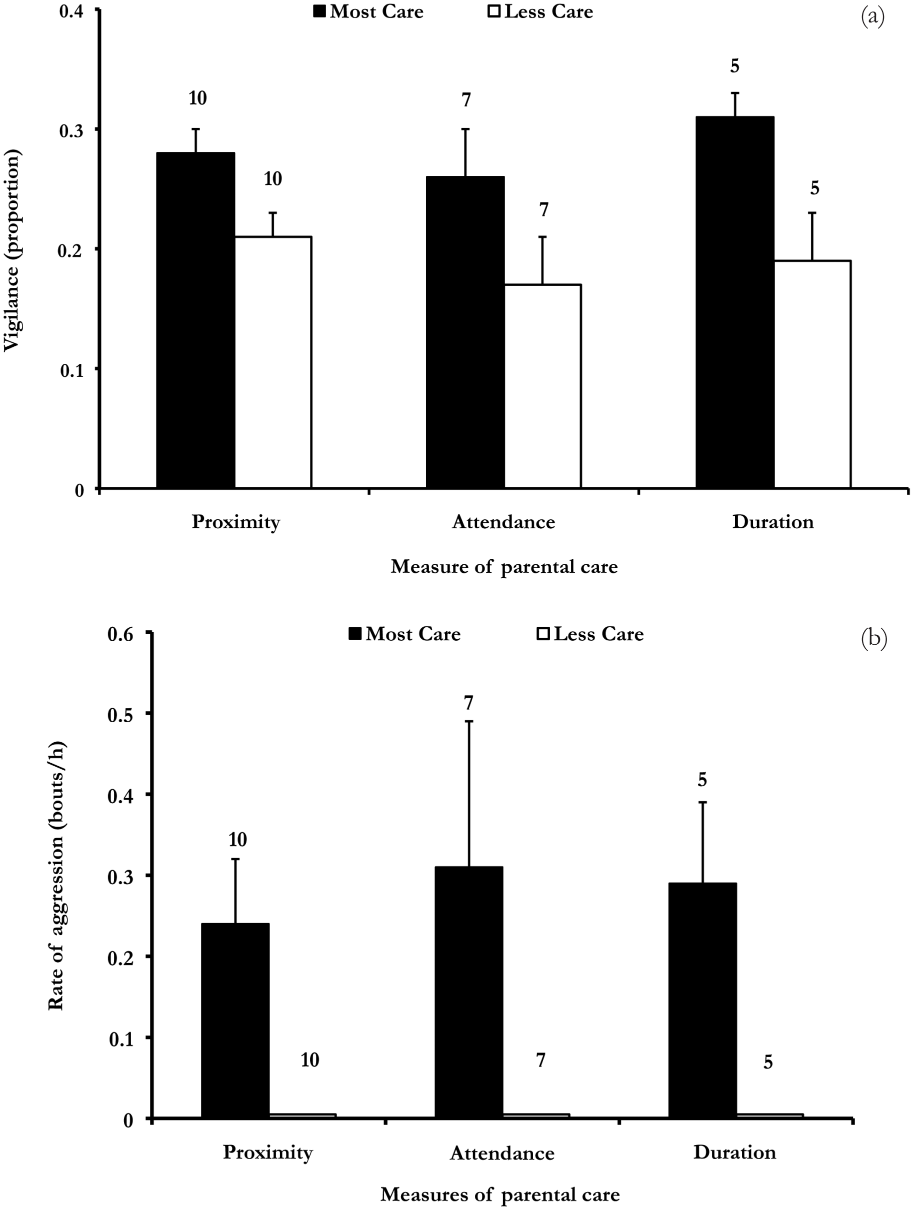

Figure 3. Average proportion of (a) vigilance and (b) rates of aggression recorded for female Western Canada Goose goslings receiving the highest amount and low amounts of parental care. Parental care was based on three measures: proximity to parents, attendance rate in family, and duration with parents into the spring. Error bars are one standard error. Sample sizes (number of families) are shown above the s.e. bars.

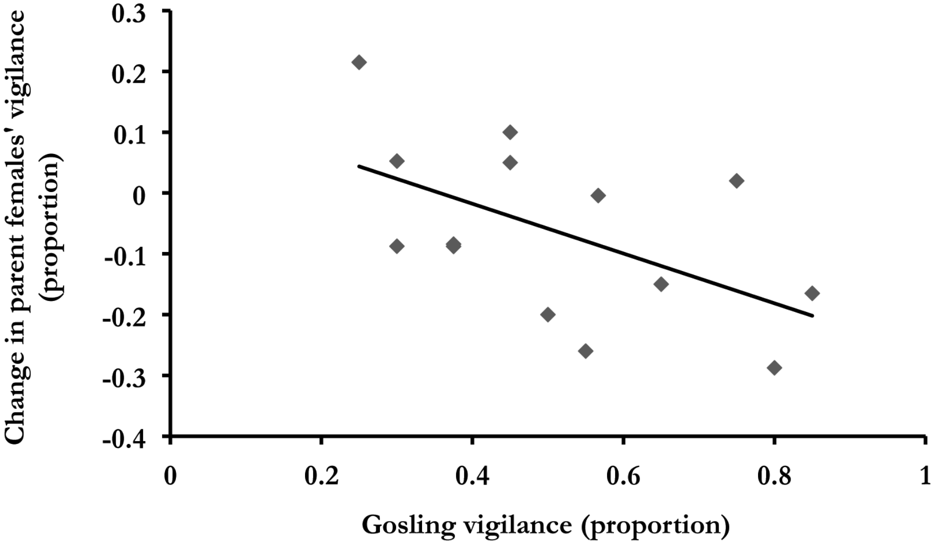

Figure 4. Relationship between the change in the proportion of time vigilant for Western Canada Goose parent females between early and late winter, and their goslings' vigilance in late winter. The mean proportion of time vigilant from the most vigilant gosling in each brood was used in the analysis.

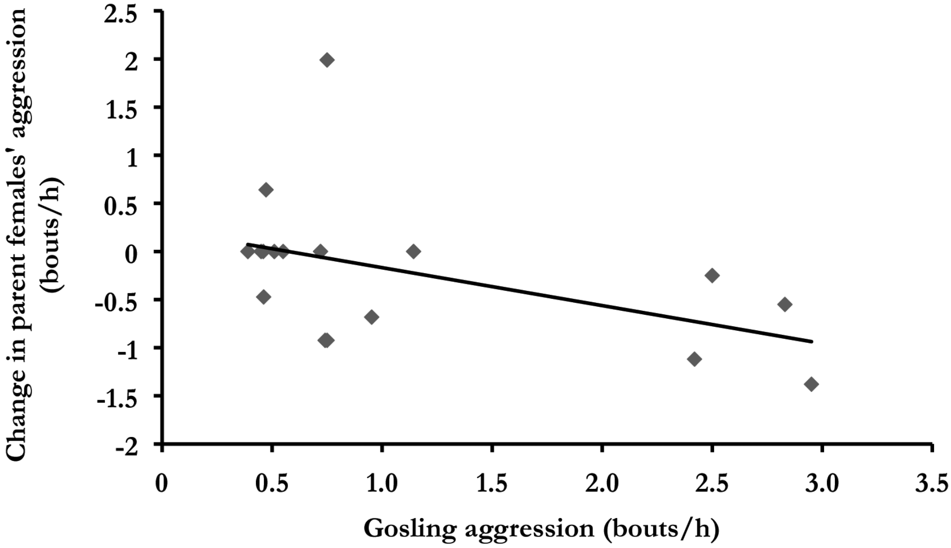

Figure 5. Relationship between the change in aggression rates recorded for Western Canada Goose parent females between early and late winter, and their goslings' aggression rates during the late winter period. The mean rate of aggression from the most aggressive gosling in each brood was used in the analysis.

(highest care) males were not significantly more aggressive than Category II (low care) males (proximity Z = 1.14, n = 10, n.s.; attendance Z = 0.09, n = 7, n.s.; no test for duration variable, n = 1). With regard to siblings' structural size, there was no significant difference in skull length between Category I and II goslings for either sex (range of results for females, for proximity, attendance and duration: Z = 0.13–0.68, n = 5–10, n.s.; range of results for males, for proximity and attendance: Z = 0.66–0.68, n = 8–10, n.s).

To test whether parents gained any noticeable benefit from maintaining contact with "helpful" goslings, we quantified the change in the parents' vigilance and aggression in relation to gosling "help" with these behaviours for each family. The change in the female parents' level of vigilance and aggression in late winter was negatively correlated with most "helpful" goslings' level of vigilance and aggression (vigilance, r_s = –0.58, n = 14, P = 0.03, Fig. 4; aggression, r_s = –0.56, n = 17, P = 0.01, Fig. 5). These relationships were not found for male parents and their goslings.

Discussion

This study contributes to our understanding of how parental care is allocated within goose families. When both sexes were present in broods, parents maintained contact with male more than female offspring. This was notable for all three parental care measures: proximity, attendance and family duration through the first year, indicating that males received more of the benefits from parental care than their female siblings. In Barnacle Geese, long-term benefits from longer periods of parental care experienced in the first year was observable in males, but not in females, on considering the individuals' survival and eventual reproductive success (Black *et al.* 2014). Raveling *et al.* (2000) similarly documented higher rates of survival for immature Giant Canada Geese *Branta canadensis maxima* which had continued to associate with family members, in comparison with single goslings that fended for themselves in winter flocks. When associating with parents, goslings may learn social and predator detection skills, diet preferences and intricate features of foraging areas, breeding colony attributes, and landscape features along migration routes (Owen 1980; Raveling 1981; Marshall & Black 1992; Black & Owen 1989a; Black *et al.* 2014). Goslings may also assume the dominance status of their parents through association with these reproductively successful adults (Black & Owen 1984, 1989a,b; Raveling 1970). Future studies could test in further detail the occurrence and mechanism of such social inheritance in goose flocks (*sensu* Raveling 1970; Black & Owen 1987).

We are not certain whether male goslings maintained proximity and stayed longer than females in the family group as a result of parental choice or because these male goslings pushed siblings away. However, since this (and other studies) showed that maturing male goslings were significantly larger, more vigilant and more aggressive than female siblings (Table 2), it is likely that a sibling-sibling hierarchy was established within families (*sensu* Black & Owen 1987). In Barnacle Geese, goslings experienced an increasing number of parental attacks, which came mostly from male parents, but also from female parents and dominant siblings (Black & Owen 1989a). The only way that goslings are able to withstand these attacks is to employ a submissive "greeting" posture that subdues the aggressor (Radesäter 1974). Goslings use this behaviour when they approach or get approached by a parent or dominant sibling. Black *et al.* (2014) provided limited, but compelling evidence that male Barnacle Goose goslings were consistently closer, and were attacked least by parents. Furthermore, Black & Owen (1987) described that a rank order existed among siblings within broods, where males were eventually dominant over females as males grew larger in structural size.

The question remains about whether parents favoured gosling males to females because males were more "helpful." To address this question, we compared the allocation of types of parental care among same-sex siblings. Within-sex comparisons among siblings suggest that parents may have allocated care based on behavioural rather than structural size. For female goslings, the more vigilant and aggressive individuals were provided more of all types of parental care (Fig. 3), and more vigilant males were provided more care in one measure (proximity to parents). Perhaps parents based investment decisions on a "threshold of helpfulness," where individuals displaying a certain level of vigilance and aggression were preferred. By nature, males tended to be more vigilant and aggressive than females, thus ensuring they were above this threshold, while only the most vigilant and aggressive females reached that threshold. This aligns with the idea that the most helpful offspring were favoured by parents, where "help" was in the form of gosling contributions toward watching for competitors and predators and maintenance of foraging space within flocks.

In some earlier studies of birds and mammals, parents have been found to attribute more care to weaker or smaller individuals, whereas in others parents favoured the larger, stronger individuals (Stamps *et al.* 1985; Clutton Brock 1991; Slagvold 1997; Lessells 2002). Our own study found that measures of parental care in Western Canada Geese did not vary according to gosling structural size (*i.e* skull length) within each of the sexes.

Results from this study contribute to understanding why some parents maintain contact with goslings well into the late winter and spring, while attempting to rebuild body stores for the next breeding season (*sensu* Black & Owen 1989a). Female Western Canada Goose parents spent less of their day being vigilant and chasing conspecifics when their families contained helpful offspring. This was determined by calculating the change (or reduction) in female parent's vigilance and aggression as the maturing offspring increased their own effort in watching and chasing flock members. These finding are in line with predictions from the "*Gosling Helper Hypothesis,*" which suggested that parents would benefit from gosling help (*sensu* Black & Owen 1989a). However, the largest benefit to parents measured to date was only for females which continued their association with the most vigilant and aggressive goslings in the family.

While some of the "resident" Western Canada Geese in this study have flown north to moult in summer (~20%; Griggs & Black 2004), most remained in the same general area around Humboldt Bay, California throughout the year. In all cases, the period of parent-offspring association at Humboldt Bay ended when parents began a new nesting attempt in early spring. This occurred when the mature goslings were 10–11 months old. In contrast, geese that migrate to northern breeding grounds may arrive there with mature goslings still in tow (*e.g.* Prevett & MacInnes 1980). In Greater White-fronted Geese *Anser albifrons*, mature offspring (yearlings) fitted with neck-collars have been resighted on their parents' territories (Ely 1979). Warren *et al.* (1993) suggested that yearlings may provide a form of "alloparental" care by helping to defend territorial boundaries on the breeding grounds. Fox *et al.* (1995) quantified time spent foraging and in vigilant postures for White-fronted Goose pairs on arrival prior to nest establishment, and found that pairs with yearlings still in association spent more time foraging and less time vigilant than pairs without yearlings, which lends further support to the "helper" hypothesis. The authors went on to propose (on page 155 of Fox *et al.* 1995) that maturing goslings experience a "developmental switch from offspring as dependents (eliciting additional vigilance in parents during their first summer) to offspring as cooperators (sharing vigilance with parents)."

Most research in other species have emphasised the costs of parental care (Trivers 1974; Parker 1985; Clutton Brock 1991). The results described in this paper provides evidence that parents may benefit from providing care to offspring with helpful characteristics. Perhaps the mutual benefits that both parents and goslings receive lessens the conflict that may arise with extended periods of parental care in goose flocks.

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Photograph: Western Canada Goose female with brood, by Leslie Scopes Anderson.