Sex-specific behavior by a monomorphic seabird represents risk partitioning

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The presence of sex-stereotyped behavior in monomorphic animals, where there are no sexual differences in form to account for sexual differences in function, is often attributed to intraspecific competition or to differential parental investment. The possibility that the use of different behavioral strategies by each parent may increase reproductive success for both partners through risk partitioning is seldom considered. We studied thick-billed murres (*Uria lomvia*), where the male exclusively feeds the offspring during the late chick rearing. During the period of biparental care, males fed on "risk-averse" prey (consistent across time and space; unitized risk = 0.29), whereas females fed on "risk-prone" prey (risk = 0.59). Males fed at night at 1 colony, during the day at 2 colonies, and there was no pattern at another colony. We suggest that these differences reflect the availability of risk-prone prey. Modeling suggested that mixed-risk pairs had higher success than "risky" or "riskless" pairs. Males accumulated reserves and reduced chick provisioning just prior to fledging. Thus, sex-specific patterns at 1 period (male-only care during postfledging) may have led to sex-specific patterns at earlier periods through the need for specialization in foraging habits and risk. We propose that risk partitioning may contribute to the prevalence of sex-specific behaviors in monomorphic animals and that patterns are likely context specific rather than species specific. *Key words:* risk aversion, sex-specific behavior, thick-billed murre, *Uria lomvia.* [Behav Ecol 21:1024–1032 (2010)]

Biparental care is rare in animals (Mock and Fujioka 1990). Birds are unusual in this regard because although they show the complete spectrum of parental care—no parental care, male-only, female-only, and biparental care—biparental monogamy occurs in roughly 90% of birds (Lack 1968; Mock and Fujioka 1990). For sexually size-dimorphic birds, intersexual differences in foraging patterns may reflect niche partitioning to increase combined niche breadth, asymmetrical competition, or differences in foraging efficiency without direct competition (Morse 1968; Marquiss and Newton 1982; Aho et al. 1997; Weimerskirch et al. 1997; Gonzales-Solis et al. 2000). For many dimorphic species, the differences in foraging behavior between the sexes are continuations of size-related differences in foraging behavior that occur within each sex (e.g., Zavalaga et al. 2007). For example, larger marine animals can dive deeper, catch larger prey, or exclude smaller conspecifics from foraging areas (Halsey et al. 2006; mammals: Beck et al. 2003; Baird et al. 2005; Page et al. 2005; penguins: Bethge et al. 1997; Clarke et al. 1998; cormorants: Kato et al. 2000; Ishikawa and Watanuki 2002; Cook et al. 2007; boobies: Weimerskirch et al. 2006; albatrosses: Weimerskirch et al. 1997). Nonetheless, if sex-specific differences in foraging were driven by sex-specific differences in form through competition or efficiency, then, we would not expect there to be sex-specific differences in foraging in monomorphic animals. In contrast, many monomorphic seabirds with biparental care show sex-stereotyped foraging behavior (Table 1).

There are several explanations for sex-stereotyped foraging behavior in monomorphic animals (Table 1), but implicit in most explanations is the idea that having both parents maximize energy delivered to the chick maximizes chick growth

and, therefore, reproductive success. Thus, explanations tend to account for reduced "investment" of 1 parent through carryover effects during future or past periods, variation in their response to chick begging or intrasexual competition, or by considering that the investment of 1 partner is actually in chick defense (Table 1). That having 2 parents forage in the same manner may not maximize reproductive success is seldom considered. For example, risk partitioning can increase fitness because the risk-averse partner may provide enough food to ensure that the chick reaches fledging (especially during periods of shortages), whereas the risk-prone partner may provide the extra bulk for improved postfledging survival; a pair consisting only of risk-averse birds may be able to consistently fledge chicks but with low body mass and low postfledging survival, whereas a pair consisting of only risk-prone birds may often fledge chicks with high postfledging survival but may also be unable to fledge chicks in poor years. Risk partitioning may provide the evolutionary explanation for why 1 sex is sometimes less sensitive to chick begging than the other sex (Quillfeldt et al. 2004) and is just 1 example of many potential combinations of context-dependent foraging whereby having 2 members of the pair foraging in the same manner may not maximize reproductive success (including where 1 sex targets a specific nutrient).

Risk is an important component of foraging decisions as individuals may choose less nutritive but more consistent food sources over more nutritive but less consistent food sources to avoid the risk of starvation or because several small "snacks" are easier to digest than 1 large meal (Karasov and Diamond 1988; Wu and Giraldeau 2005; Eccard and Liesenjohann 2008). Unitized risk (standard deviation divided by mean or coefficient of variation) is a relative measure of variability, has been shown to be a better account for patterns of risk sensitivity than absolute variability (Shafir 2000), and is widely used to quantify risk in ecological systems (e.g., Abreu and Kacelnik 1999; Bateson 2002; Dubois and Giraldeau 2003). Foraging risk is likely to play a strong role in the marine environment

Table 1

Sex-specific differences in chick-provisioning behavior during the breeding season among monomorphic birds (<5% difference in main linear size parameter reported in each paper)

Species	Provisioning rate	Cause	Other differences	References
Thin-billed prion	M = F	NE		Quillfeldt et al. (2004)
Manx shearwater	M > F	CB	T	Gray and Hamer (2001); Quillfeldt et al. (2004)
Wedge-tailed shearwater	M > F	IC	D, T	Peck and Congdon (2006)
Wilson's storm petrel	M = F	CB, IC		Gladbach et al. (2009)
Northern gannet		COE, IC	D, S	Lewis et al. (2002)
Black-necked stilt	M > F[a]	ND		Sordahl (1990)
Eurasian lapwing	M > F[a]	ND		Hehgy and Sasvari (1998)
Common tern	M > F[b]	IC		Wiggins and Morris (1987); Wagner and Safina (1989)
Roseate tern	M > F			Wagner and Safina (1989)
Forster's tern	M = F	NE		Bluso-Demers et al. (2008)
Common murre	M < F, M > F[c]	COF	T	Thaxter et al. (2009)
Common murre	M < F, M > F[c]	PI		Cameron-Macmillan et al. (2007)
Thick-billed murre	M ≤ F, M > F[c]	RP	D, T, L	This study
Thick-billed murre	M ≤ F, M > F[c]	ND	D, T, L	Paredes et al. (2006), 2008; Paredes and Insley (2009)
Razorbill	M = F, M > F[c]	ND	D, T, L	Paredes et al. (2006), 2008; Paredes and Insley (2009)
Dovekie	M > F	COE, COF	T	Welcker et al. (2009)
Crested auklet	M < F	ND		Fraser et al. (2002)

Cause attributed by the authors = COF (carryover effects during fledging mean that 1 sex spends more time on self-maintenance or targeting specific nutrients); COE (carryover effect from egg laying means that the female spends more time on self-maintenance or targeting specific nutrients); IC (intrasexual competition leads to 1 sex outcompeting the other); ND (nest defense: 1 sex is better at defending the chick/nest and so spends more time at the nest and provisions less to balance costs); CB (1 sex regulates food provisioning in response to chick begging to a higher degree than another sex); RP (risk partitioning between the sexes); EQ (sexes are equally capable); PI (differences in parental investment); NE (no effect, so needs no explanation). Other differences = trip duration (T); dive depth (D); selectivity in foraging areas or size of core foraging range (S); diel patterns in foraging (L). M, male; F, female.

[a] Male does not provision but guards the chicks so that they provision themselves.

[b] More deliveries in 1 study and longer fish in the other.

[c] Male-only care once the chick leaves the breeding site.

where the trade off between prey quality and variability (Litzow et al. 2004) means that specializing in quality is likely to result in increased variability in foraging success (Burke and Montevecchi 2009). For example, large schooling fish have high energy content but require more above-water searching than small invertebrates (Elliott, Bull et al. 2009), and longer search times imply less frequent encounters and higher unitized risk in energy delivery rates.

Auks of the tribe Alcini (*Uria*, *Alca*, and *Alle*) are monomorphic, and incubation and chick rearing are split roughly equally up to the time of chick departure, yet the male takes the chick to sea and rears it to adulthood (1–2 months), whereas the female remains at the breeding site for a period and then departs alone (in *Alle*, the chicks depart at near-adult size, but the male still does most of the chick rearing after about 2 weeks; Harding et al. 2004; Paredes et al. 2006, 2008). Sex-specific pre- and postfledging parental care in the Alcini has been attributed to increased male aggressiveness because parental protection of offspring is thought to play a key role in successful fledging; males are slightly larger with larger bill gapes than females and more aggressive toward conspecifics (Paredes et al. 2006, 2008; Paredes and Insley 2009). Males may also play a stronger role in nest defense than females in auk species where both parents rear offspring to full body size (Fraser et al. 2002). Alternatively, female-biased prefledging parental care in the Alcini has been considered a consequence of male-biased postfledging parental care (Thaxter et al. 2009). Given the unusual patterns observed within the Alcini, we used thick-billed murres (*Uria lomvia*) as a model species to examine parental roles in monomorphic animals. Although other authors have referred to murres as being slightly dimorphic due to the 4% difference in bill size (5.9 cm for females

compared with 6.1 cm for males; Paredes et al. 2006, see also Stewart 1993) and apparent differences in body mass (Cameron-MacMillan et al. 2007; but see Gaston and Hipfner 2000), we consider them monomorphic because these differences are small and there is no difference in the first principle component of body size (Stewart 1993). We collected detailed information on chick provisioning over 15 field seasons at a colony in the Canadian Low Arctic, and, because most other studies occur at a single colony (Paredes et al. 2006, 2008; Cameron-MacMillan et al. 2007; Thaxter et al. 2009), we also collected data at 2 other colonies. We investigated how males and females differed in behavior and whether these differences likely related to nest defense, foraging efficiency, postfledging parental care, and/or risk partitioning.

MATERIALS AND METHODS

Observations were made on 30–60 pairs of murres at Coats Island (lat 62.95°N and long 82.00°W, 1995–2009), Digges Island (lat 62.55°N and long 77.58°W, 2008), and Prince Leopold Island (lat 90.00°N and long 74.00°W, 2008–2009), Canada during 1995–2009 (Gaston et al. 2005). We also compare our observations with those collected at the nearby Gannet Islands (lat 53.56°N and long 56.32°W, 2000–2003) to see if patterns emerge among colonies of different sizes and at different latitudes. Each year, at least 3 continuous all-day observation sessions of chick feeding were made from an observation blind at close range (<5 m) by teams of observers and were used to estimate energy delivery rates (details in Hipfner et al. 2006; Elliott, Woo et al. 2008). Individuals were identifiable by leg band color combination. We deployed cylindrical LOTEK 1100LTD time–depth–temperature recorders

(TDRs; Lotek Marine Technology, St John's, Canada; mass = 4.5 g, diameter = 1 cm, length = 3.3 cm, sampling interval = 3 s, total error = ±2 m) on murre legs (Coats—2004: $n = 23$, 2005: $n = 33$, 2006: $n = 80$, 2007: $n = 37$, 2008: $n = 30$, 2009: $n = 33$; Digges—2008: $n = 35$; Prince Leopold—2008: $n = 14$, 2009: $n = 11$). We corrected for drift using a custom-built Excel macro, and dives <3 m were ignored. Whereas back-mounted TDRs are known to impact murre provisioning rates (Hamel et al. 2004, Paredes et al. 2004; Elliott et al. 2007; Elliott, Woo et al. 2008), our smaller leg-mounted devices had no measurable effect (Elliott, Davoren et al. 2008). We used the temperature log from the TDR to determine whether the bird was on the water, in the air, or at the colony (Elliott, Davoren et al. 2008). Foraging behavior occurs along 3 major axes (Elliott, Davoren et al. 2008), representing prey depth (dive depth), benthic or pelagic foraging (dive shape), and distance (flight time). All other foraging variables are closely correlated with 1 of the 3 parameters so that we could account for most of the variability in foraging behavior by measuring dive depth, dive shape, and flight time.

Blood sampling

We collected brachial blood samples from parental murres and their chicks in 2003, 2006, and 2007 ($N = 114$ birds). Adult blood samples were collected in unheparinized (2003 and 2006) or heparinized (2007) cryovials and immediately centrifuged. Heparinization had no effect on stable isotope values (Woo et al. 2008). Centrifuged samples were kept frozen until freeze-dried and sent to the University of Winnipeg Stable Isotope Laboratory for analysis of carbon and nitrogen isotopes. Because carbon and nitrogen values were correlated (Woo et al. 2008), we only analyzed nitrogen values. We also collected a drop of blood from the tarsal vein on filter paper. DNA was extracted from the filter paper by excising a 3 mm spot and suspending it in 100 μl 5% Chelex solution (Sigma-Aldrich, St Louis, MO). The samples were vortexed thoroughly and incubated at 95 °C for 10 min. Sex was determined by polymerase chain reaction using the P2/P8 primer set as previously described (Griffiths et al. 1998). We also determined the sex of 28 birds independently by noting copulation position, and all 28 birds were assigned the same sex using molecular sexing technique.

Statistics and modeling

Using data collected above from Coats Island (see Results for input values), we created a model in Visual Basic to determine whether risk partitioning could increase pair fitness. Because unitized risk (see Table 2) for male thick-billed murres was 0.29 ("risk averse") and for females was 0.59 ("risk prone"), we considered a range in unitized risk varying between 0.29 and 0.59. We allowed each partner to have unitized risk = 0.29–0.59 in 0.03 increments for a total of 11 categories for each partner (11×11 categories = 121 total combinations). For each combination of unitized risks, we created a random normal distribution of feeding rates for 2^{16} partners such that the average feeding rate for both Partner 1 and Partner 2 was 144 kJ/day (the average energy delivery rate for our population). As we considered the distribution of mean energy delivery rates, the distribution is necessarily normal according to the central limit theorem. The variation in unitized risk altered the width of the distribution for each partner without changing the mean. We then calculated reproductive success to recruitment, M, for each chick using the formula:

Table 2

Average energy delivered per day and unitized risk in energy delivered per day across years (equivalent values in feeds/day in parentheses) and stable isotope (δN^{15}) values for thick-billed murres at Coats Island 2003–2007

	Females	Males
Energy delivered (kJ/day)	164 ± 6 (5.1 ± 0.4)	124 ± 2 (4.9 ± 0.4)
Unitized risk	0.59 ± 0.06 (0.36 ± 0.06)	0.29 ± 0.07 (0.21 ± 0.06)
Chick rearing (δN^{15})	*15.52 ± 0.05*	**15.32 ± 0.06**
Incubation (δN^{15})	**15.29 ± 0.07**	**15.27 ± 0.09**
Chick	*15.60 ± 0.12*	

Isotopic values not significantly different from one another are shown in bold or italics.

$$M = \alpha(DE_1 + DE_2),$$

where α converts average daily energy delivery rate into reproductive success to recruitment (based on the correlations between energy delivery rates and chick mass at fledging and between chick mass at fledging and recruitment rate; Steiner U, Smith P, and Gaston A, unpublished data), E_n is the energy delivered by partner n, and D is the digestibility that we assumed to range linearly from 0.70 for large meals (>325 kJ/day) to 0.85 for small meals (<150 kJ/day). We also removed one-fifth of meals >325 kJ/day because large meals are left uneaten by birds <3 days old (i.e., we assigned values of 80% [260 kJ/day] to prey deliveries greater than 325 kJ/day). Note that α = 0 when energy delivery rates are below that needed for chicks to grow.

All other statistical analyses were completed in R 2.4.1. To account for specialization, birds were not used in multiple years for analyses of foraging behavior and the specialization program IndSpec.Exe (Bolnick et al. 2002) was used for dietary analyses at Coats Island. Only items that were identified were used for analyses (missed prey items were ignored). The only exception were for calculations of unitized risk and energy delivery rates at Coats Island, in which case, we calculated the average value across years for each individual.

Prey items were divided into 2 categories: risk prone—deepwater benthic fish, primarily *Triglops* sculpins, and all schooling fish; risk averse—invertebrates and shallow-water benthics based on search behavior for each group (see Elliott, Bull et al. 2009; Elliot, Woo et al. 2009; Gaston et al. 2003 for more information on prey taxa). We assumed that prey requiring greater search times had lower encounter rates and were therefore "riskier." As searching occurs both underwater and above water (Elliott, Bull et al. 2009), we considered prey requiring substantial searching above water (schooling prey) or below water (deepwater benthic) to be risk prone. Wi values output from IndSpec.Exe were used to determine individual specialists for each of these groups (Bolnick et al. 2002), and the proportion of specialists for each group within each sex was compared.

RESULTS

Fitness (reproductive success to recruitment) showed a "saddle-shaped" distribution relative to risk partnerships (Figure 1). Thus, partnerships involving 1 risk-averse and 1 risk-prone member increased fitness over entirely risk-prone or entirely risk-averse partnerships (Figure 1). Feeding rates for males were similar to females (kJ/day: $t_{32} = 1.73$, $P = 0.09$; feeds/day: $t_{32} = 0.11$, $P = 0.92$; Table 2), but unitized risk across years
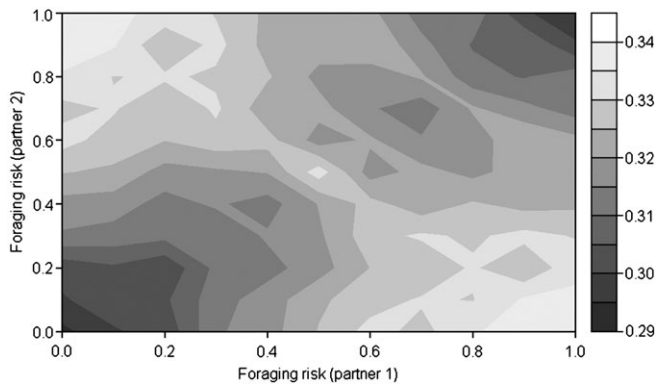
Figure 1
Postfledging survival for pairings involving birds using different levels of foraging unitized risk. Values are based on data presented for thick-billed murres with risk = 0 defined as coefficient of variation in foraging rate = 0.29 and risk = 1 defined as coefficient of variation in foraging rate = 0.59. Average survival to breeding at Coats Island is 30–40% (Table 5 in Gaston et al. 1994).

was lower for males than for females (kJ/day: $t_{32} = 3.08$, $P = 0.004$; feeds/day: $t_{32} = 2.27$, $P = 0.03$). Behavior was strongly sex stereotyped, but sex roles varied from colony to colony (Figure 2). At Coats Island, females fed the chicks and lost mass more than males, whereas males spent more time at the colony and more time submerged than females, although all differences were only statistically significant after day 15 (Figure 3).

Of 122 breeders at Coats, 107 were classified as specialists: no females and 5 males specialized on invertebrates, 1 female and 9 males on shallow benthic fish, 12 females and no males on deep benthics, and 53 females and 24 males on schooling fish. Thus, females tended to use a risk-prone strategy (taking deep-water benthic and schooling fish) when feeding chicks more often than males (which preferred shallow-water benthics and invertebrates; Fisher's Exact test: $P < 0.000001$). There was no difference in the relationship between surface pauses and depth, bottom time and dive depth, and dive depth and duration between males and females for a given time of day (analysis of covariance; all $P > 0.4$). Rather, variation in foraging behavior occurred through variation in diel foraging cycles (the sex that fed at night averaged shorter and shallower dives, shorter surface pauses, and shorter bottom times at Coats and Prince Leopold Islands, $P < 0.001$) and above-water searching (flying).

Based on stable isotope analyses, males and females at Coats Island fed themselves at similar trophic levels during incubation ($t_{64} = 1.00$, $P = 0.32$), but females switched to feeding themselves at a similar trophic level to their chicks during chick rearing (female incubating vs. female chick rearing: $t_{114} = 2.70$, $P = 0.008$; chick vs. female chick rearing: $t_{114} = 1.22$, $P = 0.23$), whereas males did not change trophic level between incubation and chick rearing ($t_{44} = 0.59$, $P = 0.54$; Table 1). Dive depth and flight time were all much more strongly bimodal for males during chick rearing than for females, whereas dive shape and dive depth for males during chick rearing were more similar to incubation values than for females (Supplementary Material).

DISCUSSION

Risk can play a role in social foraging decisions as food sharing can be an important method for overcoming risk (Dubois and Giraldeau 2003; Wu and Giraldeau 2005). We show that risk

can play an important role in even the smallest of social groups, the pair, as risk partitioning can increase the fitness of both partners. This is especially true in the marine environment due to the prey quality–variability trade off (Litzow et al. 2004). Females selected unpredictable schooling prey, whereas males selected predictable shallow benthic and invertebrate prey, which have lower energy density (benthics) or mass (invertebrates) and so low overall energy content (Elliott and Gaston 2008). Thus, through risk partitioning, pairs were able to take advantage of a spectrum of possibilities within the quality–variability trade off. Even within benthic prey, males tended to select shallower prey than females, which require less underwater search time. Furthermore, males tended to take more prey requiring risk-averse strategies than females whether benthics were classified as all risk averse (Fisher's Exact test: $P = 0.003$), all risk prone ($P = 0.005$), or subdivided into shallow and deep categories ($P < 0.000001$).

We demonstrate that risk partitioning, an extension of niche partitioning, can lead to sex-stereotyped behavior in monomorphic animals (Figure 1). For animals with distinct foraging territories during breeding, such as raptors, pairs where each mate uses a distinct foraging strategy may have higher overall feeding rates. Niche partitioning in these cases can lead to disruptive selection on body size or foraging strategies, perhaps enhanced by sexual selection, where mates choose the appropriate mate (Marquiss and Newton 1982). It seems unlikely that this would work for species with communal foraging territories, such as seabirds, as there would be no advantage at the individual level for choosing a mate that forages in a different way. Unitized risk was 102% (kJ/day) and 72% (feeds/day) higher for females than males in our system, and the difference was much greater than the differences in average energy delivery rates (33% for kJ/day and 3% for feeds/day). In another study that followed seabirds for multiple years, there was only a 3% difference in mean feeding mass per day between the sexes but a 26% difference in unitized risk (calculated from Table 1 in Gladbach et al. 2009). In that study, males and females fed in a similar way during good (high-krill) years but responded differently during poor (low-krill) years; in poor years, males used a risk-averse strategy (short trips and small meals) and females used a risk-prone strategy (long trips and large meals). Because risk partitioning (or sex-specific context-dependent strategies) leads to higher fitness at the pair level (Figure 1), it avoids the group selection flaws that occur in the niche partitioning arguments applied to colonial animals. We suggest that risk partitioning may explain why many monomorphic birds, especially long-lived birds, have sex-specific foraging patterns.

Sex-stereotyped behavioral patterns were evident in thick-billed murres (Figures 2 and 3), as is the case with other charadriiform birds (Supplementary Material), but there were large differences in male–female diel cycles at different sites. Males were at the colony during the night at Prince Leopold and Gannet Islands (Jones et al. 2002, Paredes et al. 2006, 2008, Figure 2), whereas females were at the colony during the night at Coats Island (Figure 1) and the Isle of May (*Uria aalge*; Thaxter et al. 2009). At the largest colony studied here (Digges), there was no clear pattern, possibly because prey encounters are rarer and trips are longer at large colonies, leading to variable trip lengths and a breakdown in sex-specific schedules (Gaston and Noble 1986; Hipfner et al. 2006; Elliott, Bull et al. 2009; Elliott, Woo et al. 2009). The difference between nearby colonies (and similarities among very distant colonies) is striking and shows that such patterns are not species specific. Similarly, the small number of other charadriiform birds studied also show sex-specific diel variation in nest attendance varying from location to location (e.g., plovers: Byrkjedal and Thompson 1998, p. 186). As nest attendance
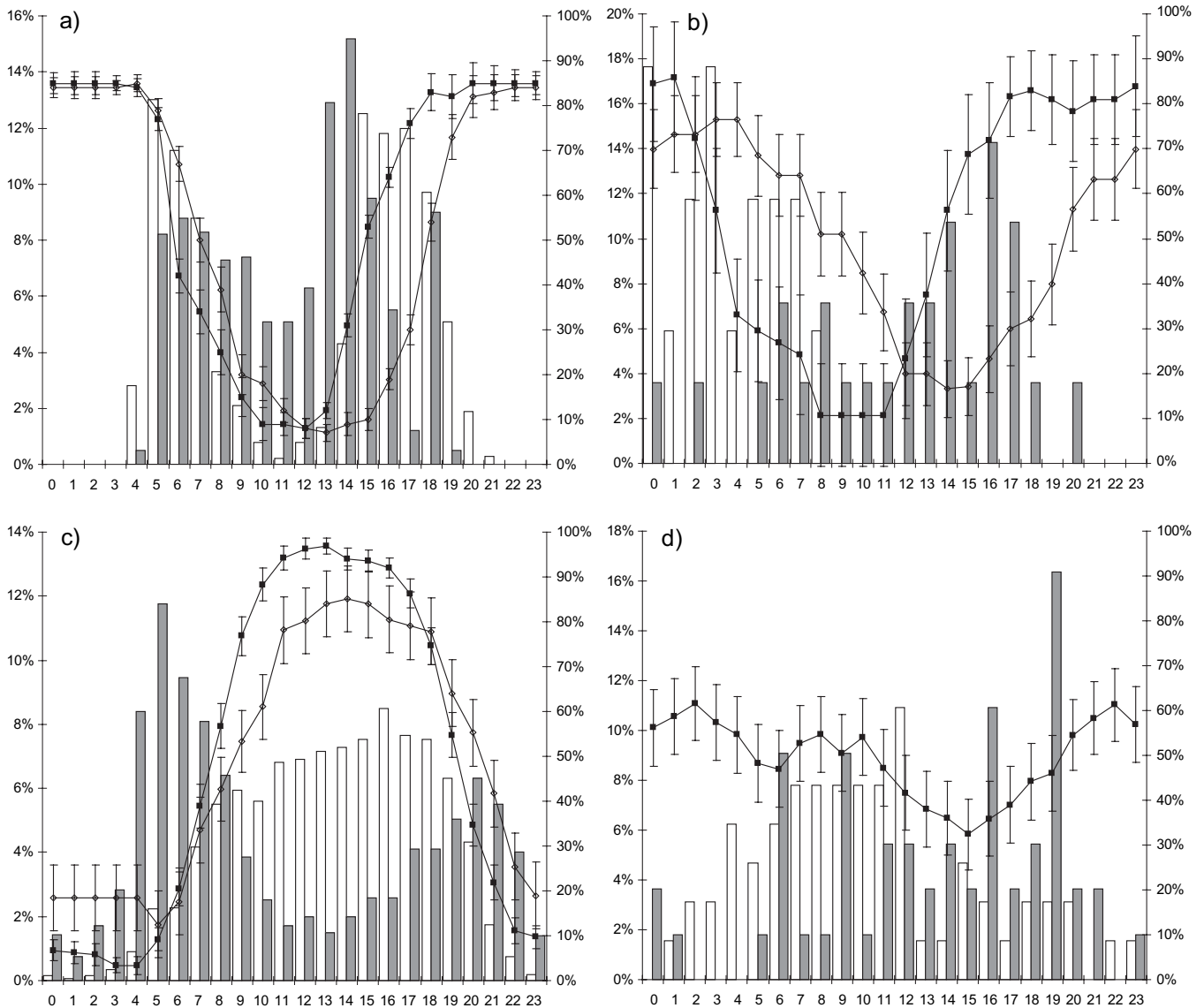
Figure 2
Proportion of time males spent at the colony during incubation (open diamonds) and chick rearing (closed squares) at (a) Gannet Islands (from Paredes et al. 2006), (b) Prince Leopold, (c) Coats, and (d) Digges. The proportion of feeds by males (gray) and females (white) are also shown.

patterns are variable, we suggest that they are likely unrelated to nest defense, which has been suggested to be the case at the Gannet Islands because the males spend more time brooding than females at that location (Paredes et al. 2006). However, the reverse is true of *U. aalge* at the Isle of May (Thaxter et al. 2009), where females spend the night with the chicks, and it seems that the difference in time spent at the colony at the Gannets is largely attributable to males being present at night at that location. At Prince Leopold Island, where there is 24-h daylight during the breeding season, both sexes spend a similar time brooding. Rather than reflecting nest defense, differences in diel cycles among colonies may represent differences in foraging opportunities, for example, the diel variation in the availability of risk-averse and risk-prone prey among different colonies. We therefore agree with Jeschke et al. (2007) that behavioral sciences need to move away from considering "species-specific" behavior to focusing on context-specific behavior.

Nest defense, and more broadly, sexual selection favoring increased male aggressiveness, has been proposed to cause larger male gape size in charadriiform birds (Wanless and Harris 1986; Creelman and Storey 1991; Jones 1993; Stewart 1993; Fraser et al. 2002; Paredes et al. 2006, 2008). Nonetheless, 1) gape size dimorphism occurs in the absence of sexual selection in some auks (Paredes et al. 2008; Berzins et al. 2009), 2) females have larger culmens even where males still have sole care for the offspring during late chick rearing, and interspecific differences in charadriiform bill morphology are believed to be related to differences in foraging behavior (invertebrate feeders have larger gapes than fish feeders among auks; Bédard 1969; Mathot et al. 2007), and 3) male and female diving seabirds are known to specialize on different foods in a consistent way across entire guilds (Bearhop et al. 2006). Therefore, we suggest that the slight sexual dimorphism in *Uria* is related to feeding differences, with males tending to feed on invertebrates and females on fish.
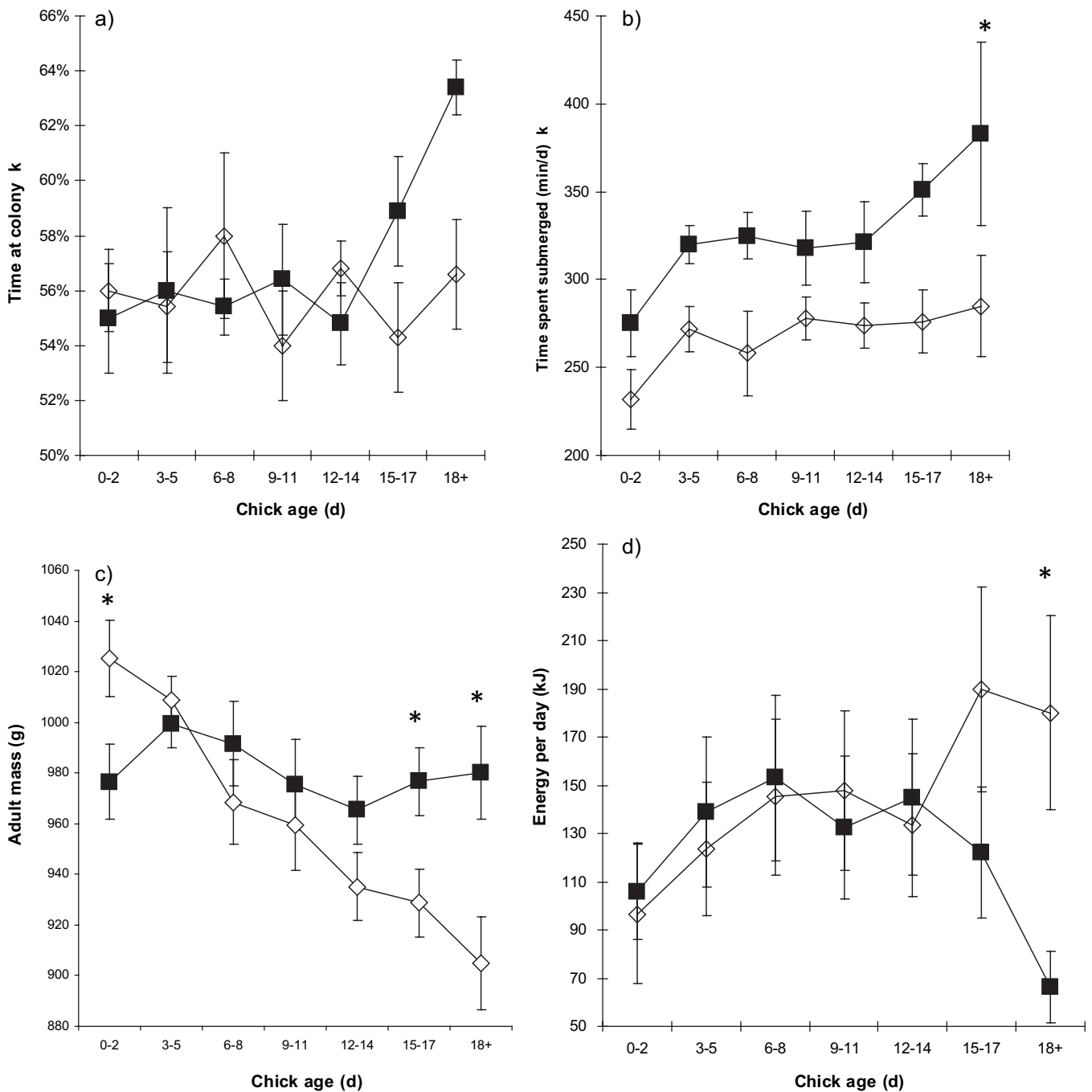
Figure 3
(a) Time spent at colony, (b) time spent submerged, (c) body mass, and (d) energy delivered to chick per day for males (filled symbols) and females (open symbols) relative to chick age for thick-billed murres at Coats Island 2004–2009.

Furthermore, although males are heavier at the time of chick departure, both sexes have a similar weight at the start of chick rearing, so it is unlikely that males are inherently heavier (see Croxall 1995 for a thorough discussion of the problems associated with using body mass to describe sexual size dimorphism). There was no difference in foraging efficiency between the sexes (see also Thaxter et al. 2009). Rather than reflecting nest defense or foraging efficiency, sex-specific roles demonstrate the impact of conditions after fledging on the behavior of males and females during chick rearing as males and females have similar attendance and

foraging patterns during the first 2 weeks of chick rearing but males feed less, spend more time with the chick, dive more, and lose less mass during the final week before fledging. At most colonies, murre feeding rates are constant during days 3–15 (summarized in Elliott, Woo et al. 2009), with females but not males provisioning at a higher rate after day 15 (Cameron-MacMillan et al. 2007; but see Paredes et al. 2008, Thaxter et al. 2009). Possibly, males need to maintain body condition for the postfledging period (Thaxter et al. 2009) and spend time with the chick to 1) increase the duration of the potential chick departure window, which

is dependent on good weather (Gilchrist and Gaston 1997) and 2) practice the cues needed for successful departure (Gilchrist and Gaston 1997). These requirements lead to more time spent brooding and self-feeding and less time chick provisioning by males, especially just before fledging (Paredes et al. 2006, 2008; Thaxter et al. 2009).

Once at sea, males need to stay in contact with the flightless offspring, and this may be facilitated by foraging for invertebrates or shallow-water benthic prey, which do not require long dives (deepwater benthic) or flying to locate ephemeral schools of fish (Elliott, Bull et al. 2009). Individual murres specialize on specific foraging strategies (and diet) across years, and it is likely that individual-specific morphological (i.e., oxygen storage capabilities) or cognitive (i.e., prey capture techniques) features and specific known foraging locations are important in maintaining foraging efficiency (Mehlum et al. 2001; Watanuki et al. 2001; Takahashi et al. 2008; Woo et al. 2008). Thus, it is likely that males specialize on the same prey items during chick rearing as during postdeparture. As schooling and deepwater prey items can be most easily captured during the day by visual predators, males are more likely to feed at night at Coats (the only site with a variety of prey fed to chicks) when invertebrates are also most available due to diel vertical migration (Garthe et al. 2007; Hedd et al. 2009). Furthermore, based on bimodal dive depth and flight time distributions, a greater similarity between dive depth and shape in incubation and chick rearing and stable isotopes, males feed themselves primarily on invertebrates during chick rearing, whereas females feed themselves on fish (which they also feed their chicks). Again, this may reflect a need for the male to forage on invertebrates postfledging. It is also a by-product of night feeding, which forces a distinct period of self-feeding; day feeding means that all foraging can be directed toward chicks (where females feed themselves on fish below a certain size or before a certain threshold and deliver them to chicks above a certain size or after a certain threshold). Thus, specialization on specific prey items maintains diel schedules across the breeding season.

Our explanation for sex-specific differences in behavior in the Alcini begs the question of why only males feed their chicks after they leave the colony. One explanation may be that male-biased parental care occurs in many other charadriiform birds, especially during late breeding, perhaps because many breed at high latitudes (with short breeding seasons) and have large eggs, and this leads to a phylogenetic bias toward male-biased parental care (Supplementary Material; Paredes et al. 2006; Paredes and Insley 2009). Thus, if the ancestral Charadriiform had male-biased parental care as a mechanism for allowing the female to replenish stores lost due to egg creation during the brief high-latitude summer, then the hormonal or neural pathways (e.g., prolactin secretion, aggressiveness) favoring male-biased parental care may preexist, and when the need for uniparental care arises again, paternal care may be favored (Paredes and Insley 2009). Once the trait "male-biased parental care" is phylogenetically fixed (i.e., the Alcini), the constraints imposed on the male by the need to keep in contact with the chick (flightlessness and shallow diving) coupled with 1) the reduction in body condition through the chick-rearing period due to reduced foraging opportunities postfledging and 2) the need for morphological or cognitive specialization together may lead to a host of behavioral differences that promote sex-specific foraging behavior, as outlined above.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

REFERENCES

Abreu FB, Kacelnik A. 1999. Energy budgets and risk-sensitive foraging in starlings. Behav Ecol. 10:338–345.

Aho T, Kuitunen M, Suhonen J, Hakkari T, Jantti A. 1997. Effects of male removal on female foraging behaviour in the Eurasian treecreeper. Behav Ecol Sociobiol. 41:49–53.

Baird RW, Hanson M, Dill ML. 2005. Factors influencing the diving behaviour of fish-eating killer whales: sex differences and diel and interannual variation in diving rates. Can J Zool. 83:257–267.

Bateson M. 2002. Context-dependent foraging choices in risk-sensitive starlings. Anim Behav. 64:251–260.

Bearhop S, Phillips RA, McGill R, Cherel Y, Dawson DA, Croxall JP. 2006. Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. Mar Ecol Prog Ser. 311: 157–164.

Bédard J. 1969. Adaptive radiation in Alcidae. Ibis. 111:189–191.

Beck CA, Bowen WD, McMillan JI, Iverson SD. 2003. Sex differences in the diving behaviour of a size-dimorphic capital breeder: the grey seal. Anim Behav. 66:777–789.

Berzins LL, Gilchrist HG, Burness G. 2009. No assortative mating based on size in black guillemots breeding in the Canadian Arctic. Waterbirds. 32:459–463.

Bethge P, Nicol S, Culik BM, Wilson RP. 1997. Diving behavior and energetics in breeding little penguins (*Eudyptula minor*). J Zool. 242:483–502.

Bluso-Demers J, Colwell MA, Takekawa JY, Ackerman JT. 2008. Space Use by Forster's Terns Breeding in South San Francisco Bay. Waterbirds. 31:357–364.

Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck R. 2002. Measuring individual-level resource specialization. Ecology. 83: 2936–2941.

Burke CM, Montevecchi WA. 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local conditions. J Zool. 278:354–361.

Byrkjedal I, Thompson D. 1998. Tundra Plovers: the Eurasian, Pacific and American golden plovers and grey plover. London, UK: A & D Poyser.

Cameron-MacMillan ML, Walsh CJ, Wilhelm SI, Storey AE. 2007. Male chicks are more costly to rear than females in a monogamous seabird, the common murre. Behav Ecol. 18:81–85.

Clarke JR, Manly B, Kerry K, Gardner H, Franchi E, Corsolini S, Focardi S. 1998. Sex differences in Adelie penguin foraging strategies. Polar Biol. 20:248–258.

Cook TR, Cherel Y, Bost CA, Tremblay Y. 2007. Chick-rearing Crozet shags (*Phalacrocorax melanogensis*) display sex-specific foraging behavior. Antarct Sci. 19:55–63.

Creelman E, Storey AE. 1991. Sex-differences in reproductive behaviour of Atlantic puffins. Condor. 93:390–398.

Croxall JP. 1995. Sexual size dimorphism in seabirds. Oikos. 73: 399–403.

Dubois F, Giraldeau LA. 2003. The forager's dilemma: food sharing and food defense as risk-sensitive foraging options. Am Nat. 162: 768–779.

Eccard JA, Liesenjohann T. 2008. Foraging decisions in risk-uniform landscapes. PLoS One. 3:e3438.

Elliott KH, Bull RD, Gaston AJ, Davoren GK. 2009. Underwater and above-water search patterns of an Arctic seabird: reduced searching at small spatiotemporal scales. Behav Ecol Sociobiol. 63: 1773–1785.

Elliott KH, Davoren GK, Gaston AJ. 2007. The influence of buoyancy and drag on the dive behaviour of an arctic seabird, the thick-billed murre. Can J Zool. 85:352–361.

Elliott KH, Davoren GK, Gaston AJ. 2008. Increasing energy expenditure for a deep-diving bird alters time allocation during the dive cycle. Anim Behav. 75:1311–1317.

Elliott KH, Gaston AJ. 2008. Mass-length relationships and energy content of fishes and invertebrates delivered to nestling thick-billed murres Uria lomvia in the Canadian arctic, 1981-2007. Mar Ornithol. 36:25–34.

Elliott KH, Woo K, Gaston AJ, Benvenuti S, Dall'Antonia L, Davoren GK. 2008. Seabird foraging behaviour indicates prey type. Mar Ecol Prog Ser. 354:289–303.

Elliott KH, Woo KJ, Gaston AJ, Benvenuti S, Dall'Antonia L, Davoren GK. 2009. Central-place foraging in an arctic seabird provides evidence for Storer-Ashmole's halo. Auk. 126:613–625.

Fraser GS, Jones IL, Hunter FM. 2002. Male-female differences in parental care in monogamous crested auklets. Condor. 104: 413–423.

Garthe S, Montevecchi WA, Davoren GK. 2007. Flight destinations and foraging behaviour of northern gannets (Sula bassana) preying on a small forage fish in a low-Arctic ecosystem. Deep Sea Res II. 54:311–320.

Gaston AJ, de Forest LN, Donaldson G, Noble DG. 1994. Population parameters of thick-billed murres at Coats Island, Northwest Territories, Canada. Condor. 96:935–948.

Gaston AJ, Gilchrist HG, Hipfner JM. 2005. Climate change, ice conditions and reproduction in an Arctic nesting marine bird; Brünnich's guillemot (Uria lomvia L). J Anim Ecol. 74:832–841.

Gaston AJ, Hipfner JM. 2000. Thick-billed Murre (Uria lomvia). In: Poole A, Gill F, editors. The Birds of North America. No. 497. Philadelphia (PA): The Birds of North America, Inc.

Gaston AJ, Noble DG. 1986. The possible effect of food availability on incubation and brooding shifts of Brunnich's guillemot Uria lomvia at Digges Island, Northwest Territories. Seabird. 9:47–51.

Gaston AJ, Woo K, Hipfner JM. 2003. Trends in forage fish populations in northern Hudson Bay since 1981, as determined from the diet of nestling thick-billed murres Uria lomvia. Arctic. 56:227–233.

Gilchrist HG, Gaston AJ. 1997. Factors affecting the success of colony departure by thick-billed murre chicks. Condor. 99:345–352.

Gladbach A, Braun C, Nordt A, Peter HU, Quillfeldt P. 2009. Chick-provisioning and nest attendance of male and female Wilson's storm petrels Oceanites oceanites. Polar Biol. 32:1315–1321.

Gonzales-Solis J, Croxall JP, Wood AG. 2000. Sexual dimorphism and sexual strategies in foraging strategies of northern giant petrels, Macronectes halli, during incubation. Oikos. 90:390–398.

Gray CM, Hamer KC. 2001. Food-provisioning behaviour of male and female Manx shearwaters, Puffinus puffinus. Anim Behav. 62: 117–121.

Griffiths R, Double M, Orr K, Dawson RJG. 1998. A DNA test to sex most birds. Mol Ecol. 7:1071–1075.

Halsey LG, Blackburn TM, Butler PJ. 2006. A comparative analysis of the diving behaviour of birds and mammals. Funct Ecol. 20: 889–899.

Hamel NJ, Parrish JK, Conquest LL. 2004. Effects of tagging on behaviour, provisioning, and reproduction in the common murre (Uria aalge), a diving seabird. Auk. 121:1161–1171.

Harding AMA, van Pelt TI, Lifjeld JT, Mehlum F. 2004. Sex differences in little auk Alle alle parental care: transition from biparental to paternal-only care. Ibis. 146:642–651.

Hedd A, Regular PM, Montevecchi WA, Buren AD, Burke CM, Fifield DA. 2009. Going deep: common murres dive into frigid water for aggregated, persistent and slow-moving capelin. Mar Biol. 156: 741–751.

Hegyi Z, Sasvari L. 1998. Components of fitness in Lapwings Vanellus vanellus and black-tailed godwits Limosa limosa during the breeding season: Do female body mass and egg size matter? Ardea. 86:43–50.

Hipfner JM, Gaston AJ, Smith BD. 2006. Regulation of provisioning rate in the thick-billed murre (Uria lomvia). Can J Zool. 84: 931–938.

Ishikawa K, Watanuki Y. 2002. Sex and individual differences in foraging behaviour of Japanese cormorants in years of different prey availability. J Ethol. 20:49–54.

Jeschke JM, Wanless S, Harris MP, Kokko H. 2007. How partnerships end in guillemots Uria aalge: chance events, adaptive change, or forced divorce? Behav Ecol. 18:460–466.

Jones IL. 1993. Sexual differences in bill shape and external measurements of crested auklets (Aethia cristatella). Wilson Bull. 105: 525–529.

Jones IL, Fraser GS, Rowe S, Carr X, Taylor P. 2002. Different patterns of parental effort during chick-rearing by female and male thick-billed murres (Uria lomvia) at a low Arctic colony. Auk. 119: 1064–1074.

Karasov WH, Diamond J. 1988. Interplay between physiology and ecology in digestion. Bioscience. 38:602–611.

Kato A, Watanuki Y, Nishiumi I, Kuroki M, Shaughnessy P, Naito Y. 2000. Variation in foraging and parental behavior of king cormorants. Auk. 117:718–730.

Lack D. 1968. Ecological adaptations for breeding in birds. London: Chapman and Hall.

Lewis S, Benvenuti S, Dall'Antonia L, Griffiths R, Money L, Sherratt TN, Wanless S, Hamer KC. 2002. Sex-specific foraging behaviour in a monomorphic seabird. Proc R Soc Lond B Biol Sci. 269: 1687–1693.

Litzow MA, Piatt JF, Abookire AA, Robards MD. 2004. Energy density and variability in abundance of pigeon guillemot prey: support for the quality-variability trade-off hypothesis. J Anim Ecol. 73: 1149–1156.

Marquiss M, Newton I. 1982. Habitat preference in male and female sparrowhawks Accipiter nisus. Ibis. 124:324–328.

Mathot K, Smith BD, Elner RW. 2007. Latitudinal clines in food distribution correlate with differential migration in the western sandpiper. Ecology. 88:781–791.

Mehlum F, Watanuki Y, Takahashi A. 2001. Diving behaviour and foraging habitats of Brünnich's guillemots Uria lomvia breeding in the High-Arctic. J Zool. 255:413–423.

Mock DW, Fujioka M. 1990. Monogamy and long-term pair bonding in vertebrates. Trends Ecol Evol. 5:39–43.

Morse DH. 1968. A quantitative study of foraging of male and female spruce-wood warblers. Ecology. 49:779–784.

Page B, McKenzie J, Goldsworthy SD. 2005. Inter-sexual differences in New Zealand fur seal diving behaviour. Mar Ecol Prog Ser. 304: 249–264.

Paredes R, Insley SJ. 2009. Sex-biased aggression and male-only care at sea in Brünnich's guillemots Uria lomvia and razorbills Alca torda. Ibis. 152:48–62.

Paredes R, Jones IL, Boness DJ. 2004. Reduced parental care, compensatory behaviour and reproductive costs experienced by female and male thick-billed murres equipped with data loggers. Anim Behav. 69:197–208.

Paredes R, Jones IL, Boness DJ. 2006. Parental roles of male and female thick-billed murres and razorbills at the Gannet Islands, Labrador. Behaviour. 143:451–481.

Paredes R, Jones IL, Boness DJ, Tremblay Y, Renner M. 2008. Sex-specific differences in diving behaviour of two sympatic Alcini species: thick-billed murres and razorbills. Can J Zool. 86:610–622.

Peck DR, Congdon BC. 2006. Sex-specific chick provisioning and diving behaviour in the wedge-tailed shearwater Puffinus pacificus. J Avian Biol. 37:245–251.

Quillfeldt P, Masello JF, Hamer KC. 2004. Sex differences in provisioning rules and honest signalling of need in Manx shearwaters, Puffinus puffinus. Anim Behav. 68:613–620.

Shafir S. 2000. Risk-sensitive foraging: the effect of relative variability. Oikos. 88:663–669.

Sordahl AT. 1990. Sexual differences in antipredatior behavior of breeding American avocets and black-necked stilts. Condor. 92:530–532.

Stewart DT. 1993. Sexual dimorphism in thick-billed murres, *Uria lomvia*. Can J Zool. 72:346–351.

Takahashi A, Matsumoto K, Hunt GL, Shultz MT, Kitaysky AS, Sato K, Iida K, Watanuki Y. 2008. Thick-billed murres use different diving behaviors in mixed and stratified waters. Deep Sea Res II. 55:1837–1845.

Thaxter CB, Daunt F, Hamer KC, Watanuki Y, Harris MP, Grémillet D, Peters G, Wanless S. 2009. Sex-specific food provisioning in a monomorphic seabird, the common guillemot *Uria aalge*: nest defence, foraging efficiency or parental effort? J Avian Biol. 40:75–84.

Wagner RH, Safina C. 1989. Relative contribution of the sexes to chick feeding in Roseate and common Terns. Wilson Bull. 101:497–500.

Wanless S, Harris MP. 1986. Time spent at the colony by male and female guillemots *Uria aalge* and razorbills *Alca torda*. Bird Study. 33:168–176.

Watanuki Y, Mehlum F, Takahashi A. 2001. Water temperature sampling by foraging Brünnich's guillemots with bird-borne data loggers. J Avian Biol. 32:189–193.

Weimerskirch HY, Cherel Y, Cuenot-Chaillet F, Ridoux V. 1997. Alternative foraging strategies and resource allocation by male and female wandering albatrosses. Ecology. 78:2051–2063.

Weimerskirch HY, Le Corre M, Ropert-Coudert Y, Kato A, Marsac F. 2006. Sex-specific foraging behaviour in a seabird with reversed sexual dimorphism: the red-footed booby. Oecologia. 146:681–691.

Welcker J, Steen H, Harding AMA, Gabrielsen GW. 2009. Sex-specific provisioning behaviour in a monomorphic seabird with a bimodal foraging strategy. Ibis. 151:502–513.

Wiggins DA, Morris RD. 1987. Parental care of the common tern Sterna hirundo. Ibis. 129:533–540.

Woo KJ, Elliott KH, Davidson M, Gaston AJ, Davoren GK. 2008. Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. J Anim Ecol. 77: 1082–1091.

Wu GM, Giraldeau LA. 2005. Risky decisions: a test of risk sensitivity in socially foraging flocks of *Lonchura punctulata*. Behav Ecol. 16:8–14.

Zavalaga CB, Benvenuti S, Dall'Antonia L, Emslie SD. 2007. Diving behaviour of blue-footed boobies *Sula nebouxii* in northern Peru in relation to sex, body size and prey. Mar Ecol Prog Ser. 336:291–303.