

Variation in Growth Drives the Duration of Parental Care: A Test of Ydenberg's Model

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ABSTRACT: The duration of parental care in animals varies widely, from none to lifelong. Such variation is typically thought to represent a trade-off between growth and safety. Seabirds show wide variation in the age at which offspring leave the nest, making them ideal to test the idea that a trade-off between high energy gain at sea and high safety at the nest drives variation in departure age (Ydenberg's model). To directly test the model assumptions, we attached time-depth recorders to murre parents (fathers [which do all parental care at sea] and mothers; $N = 14$ of each). Except for the initial mortality experienced by chicks departing from the colony, the mortality rate at sea was similar to the mortality rate at the colony. However, energy gained by the chick per day was ~ 2.1 times as high at sea compared with at the colony because the father spent more time foraging, since he no longer needed to spend time commuting to and from the colony. Compared with the mother, the father spent ~ 2.6 times as much time diving per day and dived in lower-quality foraging patches. We provide a simple model for optimal departure date based on only (1) the difference in growth rate at sea relative to the colony and (2) the assumption that transition mortality from one life-history stage to the other is size dependent. Apparently, large variation in the duration of parental care can arise simply as a result of variation in energy gain without any trade-off with safety.

Keywords: common murre, paternal care, thick-billed murre, *Uria aalge*, *Uria lomvia*, Ydenberg's model.

Introduction

The life history of many organisms represents a series of short transitions from one relatively lengthy life-history stage to the next (Werner 1986; Werner and Anholt 1993). The variation

in duration of each stage is often thought to arise as a result of a trade-off between safety and growth driven by a foraging–predation risk trade-off (Ludwig and Rowe 1990; Houston et al. 1993; Reznick et al. 2001). Indeed, such trade-offs have been proposed to govern the transition between life-history stages in a number of organisms, from insects to amphibians (Rowe and Ludwig 1991; Werner and Anholt 1993; Abrams and Rowe 1996). However, because of the difficulty of following wild animals, most of the tests of those ideas have occurred in captivity or used a comparative approach. The miniaturization of biologgers in recent years has meant that the existence of trade-offs within species can now be examined in the wild in a wide variety of organisms (Mainwaring 2016).

An important example of a life-history transition is the duration of parental care—the provisioning of offspring with energy while protecting them from predators—which varies widely in animals, from none (e.g., invertebrates/fish with external fertilization) to lifelong (some social mammals). Such variation evolves in response to parent-offspring conflict, whereby offspring benefit from increased parental investment and parents benefit from decreased parental investment in current offspring (Trivers 1974). For many animals, the period of transition from dependence to independence is associated with high mortality (Mainwaring 2016), and one would expect that the transition would be delayed as long as possible to an age where offspring are large enough to escape many predators. However, mortality risk can also be high during the period of parental care, and the relative risk of mortality during the period of parental care can be associated with the duration of parental care (Roff et al. 2005; Martin and Briskie 2009). For instance, in songbirds, those species with high nestling mortality (due to parasites or predation) leave the nest sooner than those with low nestling mortality (Ghalambor and Martin 2001; Remes and Martin 2002; Martin et al. 2011).

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Environment, phylogeny, and life history determine where the optimal duration of parental care lies within the parent-offspring spectrum, but because all three parameters often covary, it is difficult to demonstrate the importance of parent-offspring conflict in the evolution of parental care. Seabirds in the auk (Alcidae) family show wide variation in the age at which offspring leave the nest and go to sea, providing an opportunity for investigating the role of parent-offspring conflict in determining the duration of parental care (Sealy 1973; Ydenberg 1989, 2001; Byrd et al. 1991; Ydenberg et al. 1995, 1998; Gaston and Jones 1998). The group is phylogenetically closely related, has similar life-history traits (e.g., lay one or two eggs), and all forage within the marine environment (Gaston and Jones 1998). Of particular interest are members of the Alcini subfamily that use an intermediate strategy between immediate departure (i.e., precocial, as seen in the *Synthliboramphus* murrelets) and departure at full adult body size (i.e., semiprecocial, as in most other auks; Sealy 1973). In those species, the offspring leave the colony (accompanied by the father) at only one-quarter of adult body size and when they are still incapable of flight (Birkhead 1977; Gaston and Nettleship 1981). Indeed, the departure of offspring floating down from towering cliffs to wander the high seas with their fathers is a remarkable spectacle.

Ydenberg (1989) provided a model explaining the age at which auk offspring go to sea on the basis of the principles that mortality is greater at sea than at the nest but energy gain is higher at sea than at the nest. Given that mortality risk decreases with age but energy requirements increase with age, Ydenberg predicted variation in the time at which offspring go to sea on the basis of the relative rate at which mortality risk decreased and energy intake increased. Some aspects of the original model were criticized (e.g., Byrd et al. 1991; Gaston 1998). Ydenberg's (2001) model updated the earlier model to include the risk of parental mortality and provided a set of conditions where duration of parental care at the colony was nearly 0, as observed in the *Synthliboramphus* murrelets. At the time of Ydenberg's article, little was known about the movement of auks at sea both above and below water, and so the at-sea parameters crucial to the model were unknown.

We use time-depth recorders to observe the behavior of parent Arctic-breeding thick-billed murres (*Uria lomvia*) and temperate-breeding common murres (*Uria aalge*) during the postcolony period at five colonies. On the basis of the idea that postdeparture strategy is driven by general constraints with regard to safety and growth rates across the entire murre clade, we predicted that similar behavior would be recorded across both species of murres and at all five colonies. We also predicted that both chick mortality rates and energy intake would be higher at sea than at the colony (Ydenberg's model). Our study tackles three of the six areas of research proposed to be particularly fruitful in

the study of the transition from dependence to independence in birds (Mainwaring 2016): (1) research on precocial, nonpasserine birds that are difficult to follow; (2) research into trade-offs between development in the nest and accomplishment of tasks outside of the nest; and (3) research into the fitness costs and benefits of duration of parental care for the postdeparture period.

Methods

Study Species

The extant members of the Alcini subfamily include common murre, thick-billed murre, razorbill (*Alca torda*), and dovekie (*Alle alle*). We studied two species of murres in the Alcini clade: Arctic-breeding thick-billed murres and temperate-breeding common murres. For their body mass, murres have the highest flight costs of any animal and are consequently working at an energy ceiling, unable to work harder to feed their offspring (Elliott et al. 2014). Murres and razorbills are unique among birds in their intermediate departure strategy (although some pigeons depart the nest at ~60% of adult body size; Crome 1975; Robertson 1988). Miniature electronic recorders (such as time-depth recorders and geolocators) have recently been attached to murres, ascertaining their dive behavior and at-sea location (Croll et al. 1992; Benvenuti et al. 2002; Gaston et al. 2011; MacFarlane-Tranquilla et al. 2013) and the behavior of males and females after they leave the colony (Linnebjerg et al. 2013; Elliott and Gaston 2014; Burke et al. 2015; Harris et al. 2015). Both males and females are flightless (presumably moulting) for 2–3 months after leaving the colony (Elliott and Gaston 2014; Burke et al. 2015). Males initially engage in intense foraging, with many more dives per day than females, likely in response to demands of the chick (Elliott and Gaston 2014; Burke et al. 2015). Because murres reduce heart rate and body temperature and otherwise reduce costs during diving, diving has roughly the same energy costs as resting on the water's surface (Elliott et al. 2013b), although diving may incur other costs, such as physical damage associated with oxidative stress or hypoxia. Consequently, the intense diving activity by the male does not increase daily energy expenditure (Elliott and Gaston 2014; Burke et al. 2015). Males are limited by the slow swimming speed of the chick to forage at locations that they can swim to from the colony. Consequently, males are forced to make use of foraging patches, which yield a lower rate of energy intake (Elliott and Gaston 2014; Burke et al. 2015).

Fieldwork

Fieldwork was carried out on two murre species at five Northwest Atlantic colonies (table 1). The typically temperate-

Table 1: Number of birds in which depth recorders were retrieved and functioning from thick-billed and common murrens at the five colonies used in our study

Species and colony	Year	Males	Females
Thick-billed:			
Coats	2009	2	1
Kippaku	2012	1	2
Saunders	2012	1	1
Saunders	2014	3	2
Common:			
Funk	2009	1	1
Gull	2010	3	4
Gull	2011	1	1
Gull	2012	1	2 ^a
Gull	2013	1	2 ^a

Note: We report the year the recorder was deployed.

^a Groups in which female sample size was reduced by 1 to have balanced sample sizes (14 males and 14 females).

breeding common murrens were studied at Gull Island at the Witless Bay Ecological Reserve (47°16'N, 52°46'W), Newfoundland, and the Funk Island Ecological Reserve (49°45'N, 53°11'W), Newfoundland. The typically Arctic-breeding thick-billed murrens were studied at the west colony at Coats Island (63°00'N, 82°15'W), Nunavut, and at Saunders Island (76°34'N, 70°03'W) and Kippaku (73°42'N, 56°40'W), Greenland. At Gull and Funk Islands, Lotek LAT 2500 geolocation-time-depth-temperature recorders (5.9 g with attachment, ~0.7% body mass) were attached to plastic leg bands with cable ties and placed on the left leg of breeding murrens during late chick rearing (chicks >10–15 days of age). At Coats Island, we used a similar procedure but with Lotek LTD 1500 time-depth-temperature recorders. A Canadian Wildlife Service metal band was attached to the right leg at all three colonies. A total of 61 loggers were attached to birds in 2009 (Coats and Funk) and 2010–2013 (Gull). At both Saunders and Kippaku, Lotek LAT 2800 geolocation-time-depth-temperature recorders (8.0 g, ~0.9% of body mass) were attached to metal bands with cable ties and placed on the leg of chick-rearing birds. On the other leg, a Copenhagen Zoological Museum metal band was attached. Chicks were typically near departure (>10 days old). A total of 20 loggers were attached to birds in 2012 and 2014 (Saunders and Kippaku). More details of deployments are available elsewhere (Canada: Elliott and Gaston 2014; Burke et al. 2015; Greenland: Linnebjerg et al. 2013; Frederiksen et al. 2014), as our data are a subset of those presented therein.

Instrumented birds were recaptured on the nest in the following breeding season and the logger removed. All birds were sexed genetically, using a blood spot (Canada) or feathers (Greenland) collected on deployment or retrieval. Our retrieval rate was lower than similar studies that de-

ployed biologging equipment year-round on murrens (e.g., Gaston et al. 2011; MacFarlane-Tranquilla et al. 2014; Elliott et al. 2014) because (1) at Coats, a polar bear (*Ursus maritimus*) ate many of the eggs and offspring in the year following deployment, making recapture impossible (Gaston and Elliott 2013); and (2) at Gull, substantial expansion of the murre colony—likely driven by immigration of displaced breeders from adjacent colonies experiencing large-scale disturbance by bald eagles (*Haliaeetus leucocephalus*)—made many birds with loggers inaccessible. Because we obtained data from more females than males, we used data from all 14 males but randomly chose female data sets to achieve a sample size of 14 females, such that the number of males and females from each species, colony, and year was approximately equal (table 1).

Throughout the article, we avoid using the term “fledging,” which is typically used to describe the time when young murrens leave the colony. Fledging in birds usually refers to the time when young birds develop wing feathers that are large enough for flight, and young murrens cannot fly when they depart the colony. Rather, we use the term “departure” to refer to the time when offspring leave the nest and “independence” to refer to the time when offspring become independent from their parents.

Dive Data

We used temperature and wet-dry data to determine colony departure (for details, see Linnebjerg et al. 2013, 2014; Elliott and Gaston 2014; Burke et al. 2015). At Gull Island and Funk Island, pressure was recorded every 8 s when submerged below 2 m. At Coats Island, pressure was recorded every 6 s when depth was >10 m. At Saunders and Kippaku colonies, pressure was recorded every 8 or 10 s continuously (pressure was recorded initially at 4 s continuously for 1 month, but we included only every second measurement to provide consistency across time). We used the dive analysis program MT-Dive c 4.0 (Jensen) to estimate dive depth, duration, and surface intervals at Gull/Funk and a custom-written Visual Basic script to estimate those same parameters at Coats and Greenland. We included only dives >10 m because only dives >10 m were recorded at Coats. However, excluding the Coats data and including all dives >3 m had no effect on the statistical significance of any of our results related to diving. Because surface interval was strongly correlated with dive duration, we calculated the residual of surface interval on dive duration. For each dive, we calculated an index of patch quality (IPQ; Mori et al. 2002; Elliott et al. 2008; Elliott and Gaston 2014). Following Mori et al. (2002), we assumed that (1) within each dive cycle, murrens selected dive durations that maximized the ratio of energy gain to energy expended (usually termed “dive efficiency”; Ydenberg and Clark 1989); (2) energy gain increased with patch residency time (bottom

time) following a power law; and (3) energy expenditure was proportional to total time in the dive cycle. On the basis of those assumptions, we then solved for the patch quality (exponent in the power law between energy gain and patch residency time) that optimized the dive efficiency, resulting in the following equation:

$$\text{IPQ} = \ln \left[\frac{(1 + 3.18 \times 0.0191e^{0.0191 \times \text{duration}})(\text{duration} - 1.2 \times \text{depth})}{3.18e^{0.0191 \times \text{duration}} + \text{duration}} \right].$$

We decreased the depth coefficient from 1.32 (proposed by Mori et al. [2002] for thick-billed murres) to 1.2 to account for a faster descent rate of common murres. IPQ is based on only dive depth and duration, and it predicts the amount of energy brought back by parental murres to their offspring (Elliott et al. 2008). We estimated energy expenditure using the formula presented by Elliott and Gaston (2014). All dive data are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.kc65r> (Elliott et al. 2017). Dive data from Coats Island are also archived alongside Elliott and Gaston (2014).

Statistical Analyses

We compared the dive data of males relative to females using the following five parameters: dive depth, dive duration, residual surface interval on dive duration, IPQ, and number of dives per day. Except for the number of dives per day, values were averaged over each day. Including a value for each day after departure would have led to substantial pseudo-replication. Thus, we initially used only the first 3 days after departure. We included all males that remained at sea (presumably with a chick), on the basis of observations of the breeding site or the saltwater immersion sensor. To determine what parameters impacted dive behavior, we used a general linear model with IPQ and time spent diving per day as dependent variables and colony, sex, and year as independent variables. We then repeated those analyses with males believed to have lost their chick (because they returned to the colony). We used a biplot to examine loadings of different variables for each sex. Next, we completed a linear discriminant analysis on the five diving parameters to distinguish males with chicks from females. We then used the linear discriminant analysis to determine when paternal care ended and, consequently, chick mortality rates. We used *t*-tests to compare males and females on all five parameters and the discriminant.

A Modified Ydenberg's Model

We create a model based on our results. We assume (see "Results") that (1) offspring growth rates are higher at sea

than at the colony, (2) colony and at-sea mortality are similar during the period of parental care (except during colony departure), and (3) survival following life-history transitions (i.e., both colony departure and at-sea independence) is positively correlated with growth rates before each event. In support of assumption 3, Maness and Anderson (2013) reviewed all studies in birds, including data from nearly 100 species, and concluded that faster-growing chicks typically have higher postdeparture survival, even for species that use their wings to propel themselves underwater rather than for flight. Moreover, postdeparture survival increased with offspring growth in tufted puffins (*Fratercula cirrhata*), a species of auk (Morrison et al. 2008). However, there is no evidence for such a relationship with predeparture body mass in murres (Hedgren 1981; Harris et al. 1992, 2007) possibly because of the confounding effects of the postdeparture period where offspring treble in mass.

Our model is based on wing length rather than body mass because body mass asymptotes for murres near the end of the colony growth period, possibly because parents are near an energy ceiling and cannot deliver more food at the colony (Elliott et al. 2014) or possibly to reduce wing-loading during departure, necessarily leading to growth at the colony being lower than growth at sea. In addition, wing growth, not body mass, may be a more relevant parameter for postdeparture survival because (1) wing growth was a better predictor of postdeparture survival than body mass in puffins (Morrison et al. 2008); (2) auks generally stop gaining mass before departure while they direct resources into wing growth (Hipfner and Gaston 1999*a*, 1999*b*; Morbey et al. 1999; asymptote in body mass and increase in wing growth rate after day 10 in fig. 1), and young auks will maintain wing growth during periods of food stress while losing body mass (Benowitz-Fredericks et al. 2005; Takenaka et al. 2005), implying that continuing wing growth is more important to nestlings than maintaining body mass. Thus, we suggest that transition mortality for murres is linked primarily to wing length because chicks with longer wings will have a lower wing loading and higher glide ratio and be able to fly farther to sea. The main cause of death during departure—at least in colonies where the offspring cannot simply walk to the sea—is separation of the offspring from the father because the offspring collides with the cliff or an obstacle and is subsequently eaten by a predator or killed by nonbreeding murres near the base of the cliffs (Gilchrist and Gaston 1997). Likewise, our model assumes that transition mortality (survival postparental care) in auks is related to wing length because young birds often migrate long distances after departure in a relatively short window.

We propose the following model that calculates survival as a function of wing length (as indexed by wing chord) and can be used to predict when young auks will depart the nest. Growth in young seabirds, including auks, typically approxi-

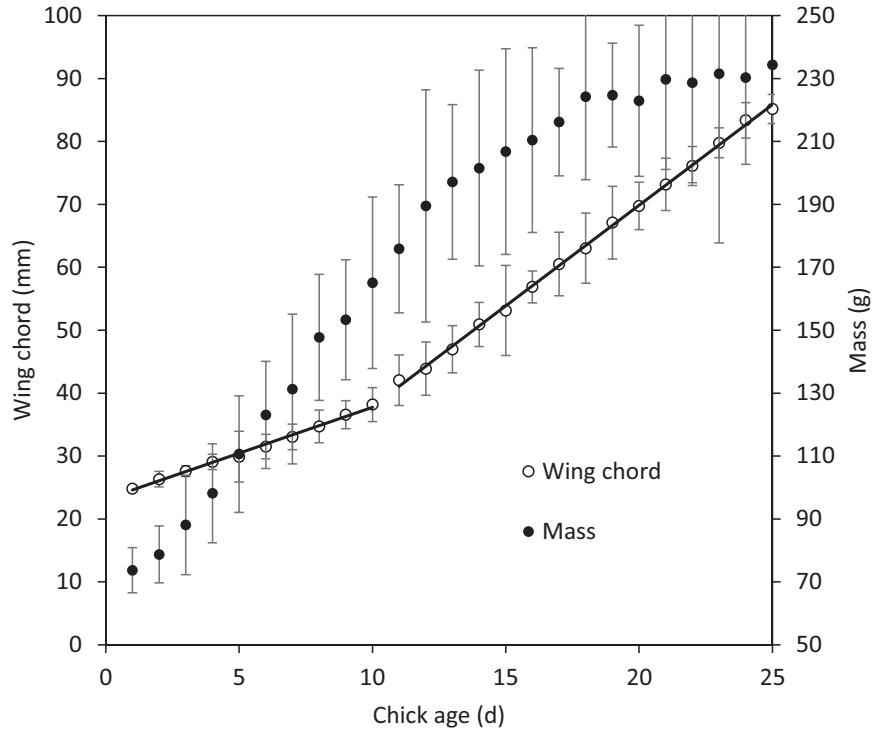


Figure 1: Average wing chord (representing the length of the primary covert) and body mass relative to age in thick-billed murre chicks at Coats Island, averaged over 15 years (1986–1999; $N = 458$ chicks; \pm SD). Solid line represents ordinary least squares regression used to estimate wing growth in the model for figure 5.

mates a von Bertalanffy growth equation (Ricklefs 1968; Barrett et al. 1987; Rodway 1997). We used a von Bertalanffy growth equation to describe wing chord, W , on date after hatching, d :

$$W_d = a + \int_{x=1}^{x=d} b(g - W_{x-1})dx \text{ if } d < c,$$

$$W_d = a + \int_{x=1}^{x=c} b(g - W_{x-1})dx + \int_{x=c}^{x=d} f(g - W_{x-1})dx \text{ if } d > c,$$

where a is initial size, b is growth rate constant at the colony, c is the duration of at-colony parental care, f is growth rate at sea, and g is the maximum wing chord length. For murrets at one of our study sites (Coats), $a = 11.61$ mm, $b = 0.0441 \text{ mm}^{-1}$ (fig. 1), and $g = 210$ mm (first year wing chord averages 204 mm in February; Gaston et al. 1983). On the basis of the estimated energy gain at sea (see “Results”), we estimated that $f = 2.1b$. Next, we consider survival to independence, S , to be a function of wing length, W , at each stage:

$$S = S(W_c)S(W_s)S_x,$$

where $S(W_c)$ is survival at time c (departure from the colony), $S(W_s)$ is survival at time s (independence from parental care, with s set at 55 days), and S_x is daily survival excluding c and s (set at 0.995 on the basis of daily survival for murrets at the colony, such that S_x was a constant of $0.995^{55} = 0.76$). Both $S(W_c)$ and $S(W_s)$ were modeled as logistic functions of wing length:

$$S_x = \frac{1}{1 + e^{-0.1(W_d - W_s)}},$$

where W_c was set at 55 mm and W_s was set at 180 mm (i.e., the inflection point was set at median values for each stage, so that survival probability was 50% of maximum when wing chord was at the given length). Note that W_c reflects the growth of the primary coverts (which are used to float down from cliffs to the sea by offspring), whereas W_s refers to the primaries (used for flight after independence).

There are no doubt additional costs to adult murrets and other auks because of high energy costs for delivering prey at the colony or high adult predation rates at the colony, which may affect the optimality of various strategies (Ydenberg 2001). Those parameters are not included in our simple model. Ydenberg’s (2001) model predicts the entire variation in auk departure strategies by incorporating variation

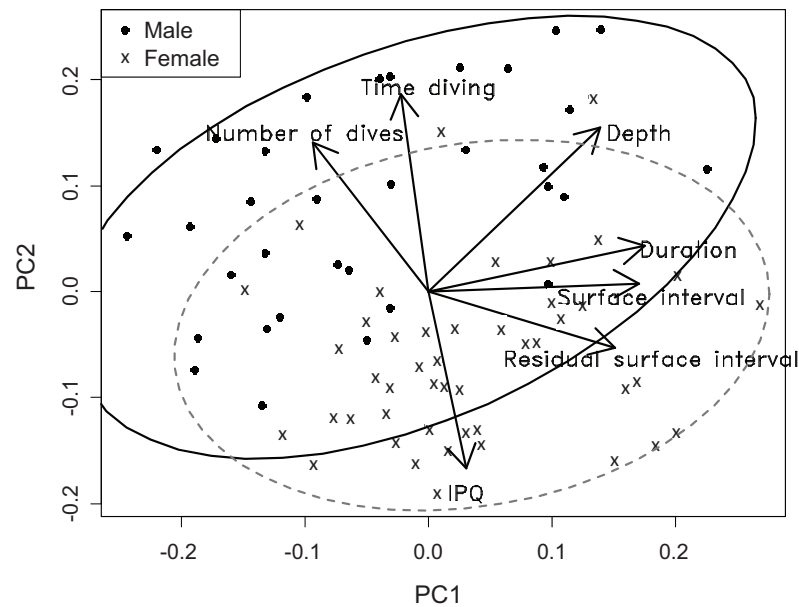


Figure 2: Principal component (PC) analysis of males and females during the first 3 days after departure. Crosses and dashed ellipse are females; circles and solid ellipse are males. Loadings for each variable are shown (index of patch quality [IPQ]).

in the rate of adult mortality. Our model predicts such variation incorporating only variation in relative energy intake at sea compared with the colony.

Results

Dive Behavior

A principal component (PC) analysis showed that males with chicks and females differed in their dive parameters (fig. 2). IPQ, dive duration, and number of dives per day strongly loaded on PC2, which separated the two sexes. We therefore concentrated subsequent analyses on those three variables, which we reduced to two variables, IPQ and time spent diving per day (the product of average dive duration and number of dives per day).

Including all females but only those males that were believed to have a chick, dive parameters averaged over the first 3 days after departure were associated with sex (time spent diving per day: $t_{18} = 2.87$, $P = .01$; IPQ: $t_{18} = 13.3$, $P < .00001$) but not colony (time spent diving per day: $F_{4,18} = 1.97$, $P = .11$; IPQ: $F_{4,18} = 1.54$, $P = .20$) or year (time spent diving per day: $F_{4,18} = 0.88$, $P = .48$; IPQ: $F_{4,18} = .80$). Thus, for all subsequent analyses, we pool all data from all colonies, years, and species. Time spent diving and IPQ were not significantly different between females and males that lost their chicks ($P > .1$; fig. 3), so we exclude males that lost their chicks from subsequent analyses.

A linear discriminant analysis applied to the first 3 days after departure classified males with 97% accuracy (one error out of 33; 11 males with chicks \times 3 days = 33 days) and females with 100% accuracy (no errors out of 42; 14 females \times 3 days = 42 days). The discriminant function was $0.27 \times \text{depth} - 0.44 \times \text{duration} - 1.25 \times \text{IPQ} + 0.22 \times \text{residual of surface interval on duration} + 1.15 \times \text{number of dives}$ (where each variable was standardized by subtracting the mean value across all individuals for the first 3 days and dividing by the standard deviation). The discriminant function classified females as having a value < -0.1 and males as having a value > 0.1 , with only one bird-day outside of those parameters; average values were approximately 1 for males and approximately -1 for females (discriminant labeled in fig. 3).

Although the discriminant function did not vary among colonies (and therefore species) within the first 3 days, the discriminant values remained positive longer for common than for thick-billed murres (fig. 4). Thus, male common murres spent more time with their chicks than thick-billed murres (fig. 4). The diving behavior of males with chicks was substantially different from that of females after departure. For both species, males had lower IPQ and more dives per day than females. Time spent diving per day increased as the chick grew, whereas IPQ stayed constant.

On the basis of a general linear mixed model with individual as a random effect and day after departure as a fixed effect, during the first 3 days after departure, IPQ was lower ($t_{62} = -5.78$, $P < .0001$; $N = 87$ murre-days), dive dura-

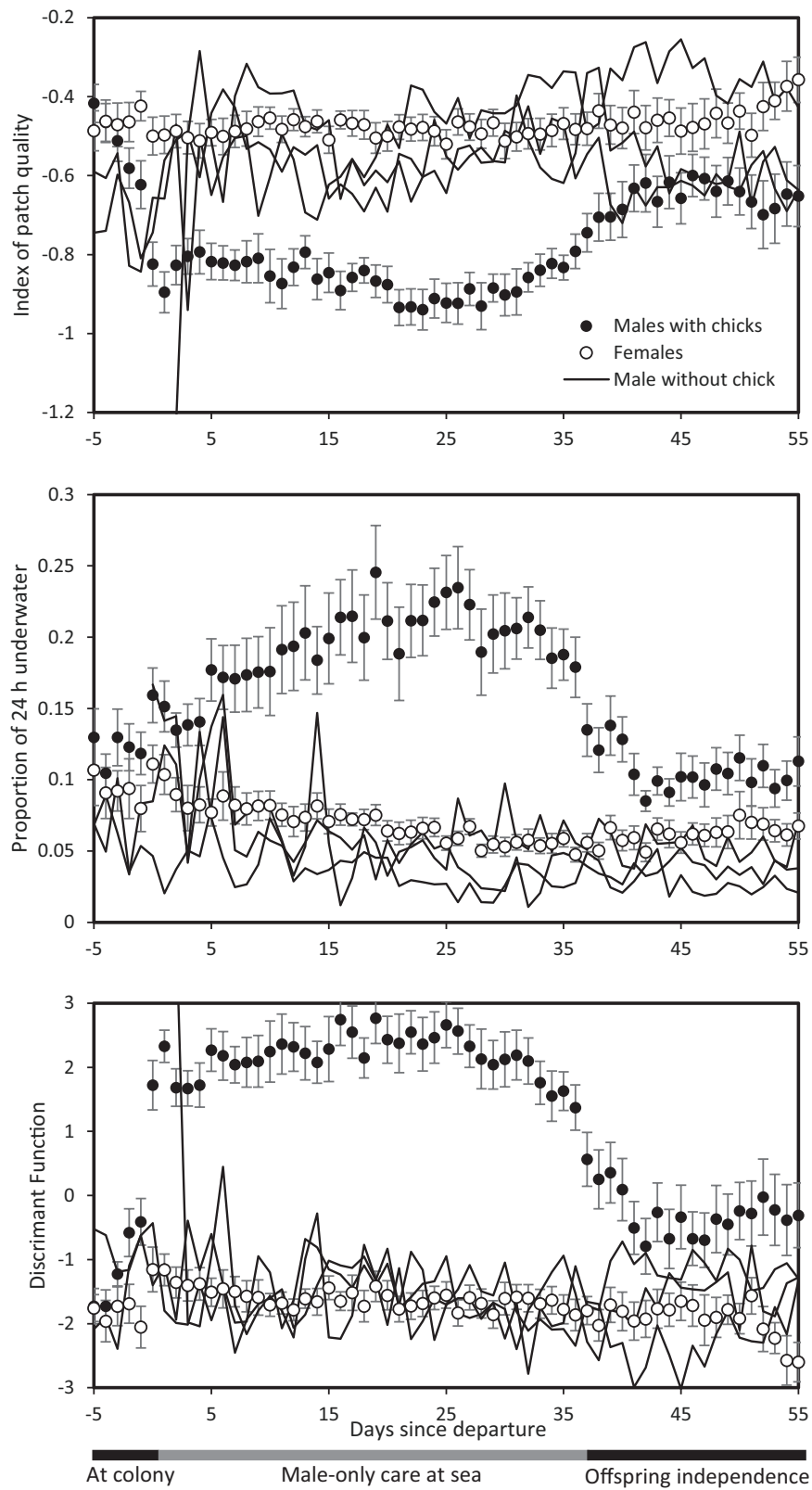


Figure 3: Index of patch quality (*top*), proportion of each 24-h period spent underwater (*middle*), and discriminant function for males with chicks (filled circles) and females (open circles; *bottom*). Also shown are individual males that we concluded lost chicks early during nest departure (lines).

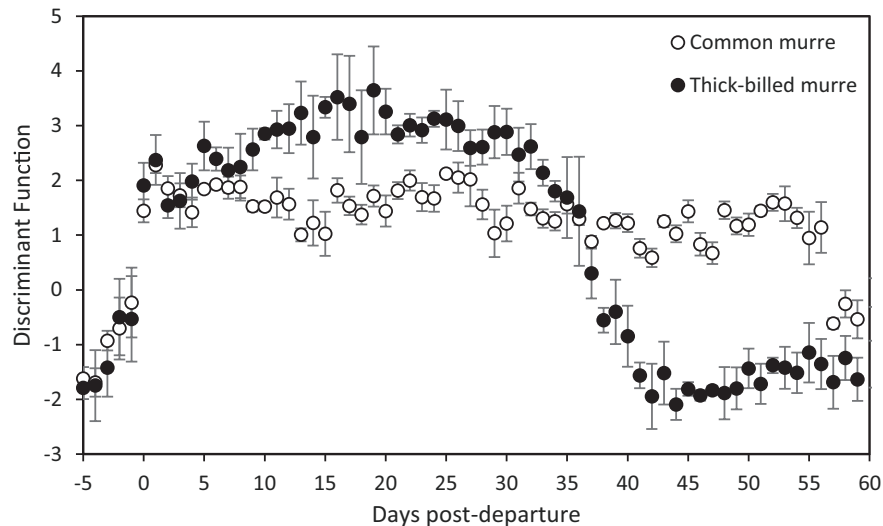


Figure 4: Discriminant function for male common (open circles) and thick-billed (filled circles) murres with chicks.

tion was shorter ($t_{62} = -2.33$, $P = .02$), and time spent diving was longer ($t_{62} = 4.03$, $P = .0002$) for males than females. In contrast, depth ($t_{62} = 0.65$, $P = .52$), daily energy expenditure ($t_{62} = 0.33$, $P = .75$), and residual surface interval on duration ($t_{62} = -1.38$, $P = .17$) was independent of sex. Over the first 30 days after the departure from the colony, daily energy expenditure averaged $1,612 \pm 9$ kJ day⁻¹ for males with chicks and $1,617 \pm 4$ kJ day⁻¹ for females.

On the basis of those results, we estimated energy intake of males and females. Males averaged ~ 290 min diving per day ($\sim 20\%$ of day), while females averaged ~ 110 min diving per day ($\sim 7.5\%$ of day). Females gained 1.5 times ($e^{0.3}$; ~ 0.3 IPQ units higher for females than males) more energy per minute diving, implying that they were eating more energy-rich food (prey with higher energy quality or in patches with higher prey density). Given that males and females had similar energy requirements, males spent approximately 165 min day⁻¹ (1.5×110 min) diving to meet their own energy demands of $1,612$ kJ day⁻¹, implying that they gained energy at 9.77 kJ min⁻¹ while diving. Assuming males fed themselves and their offspring on prey with roughly similar energy density (both males and females feed at a low trophic level, likely on invertebrates, during the flightless period; Davoren et al. 2002; Burke et al. 2015), males therefore spent the remaining 125 min of diving per day to feed their offspring $1,221$ kJ day⁻¹ (125 min day⁻¹ \times 9.77 kJ min⁻¹). Murres resting in water of 5°C (typical Arctic water temperatures in September) had ~ 1.7 times the thermoregulatory costs of murres resting at the colony at 10°C (Croll and McLaren 1993). Energy delivered to offspring at the Coats Is-

land colony averaged 336 kJ day⁻¹ (Elliott et al. 2008). Thus, taking into account the increased thermoregulatory cost, the net energy delivered to offspring (and available for growth) was still about 2.1 times the energy available at the colony ($1,221$ kJ day⁻¹ at sea compared with 1.7×336 kJ day⁻¹ at the colony, where 1.7 accounts for the increased thermoregulatory costs).

Offspring Mortality

We estimated that $\sim 21\%$ of offspring died immediately following departure, which is similar to the value of 20% recorded by Gilchrist and Gaston (1997) for mortality during departure at Coats Island. Specifically, three out of 14 males showed female-like behavior (consistent discriminant < -0.1 across many days). Two males showed complete female-like behavior, whereas the third bird had male-like behavior for the first 2 days (fig. 3). Indeed, the third bird had a discriminant function that was much higher than any of the other males with chicks for the first 1–2 days, suggesting that it may have been experiencing difficulty keeping the chick alive. It appeared that most of the mortality we observed was associated with an abortive departure, even if the chick was able to survive for an additional 24 h. Thus, in our data set, departure was among the most dangerous periods for murres. On the basis of a discriminant function consistently above 0.1, we estimated the postdeparture period at 37 ± 2 days (thick-billed murres) and 56 ± 4 days (common murres) for those individuals that survived the first 48 h.

Modified Ydenberg's Model

Our model (fig. 5) captures several aspects of auk departure strategies. First, over a range ($\pm 20\%$) of possible values for f , W_c , and W_s , the optimum value for chick departure is ~ 20 days. Second, if we assume that transition mortality is independent of wing length—which would be true of the four *Synthliboramphus* murrelets that walk to sea—then the model predicts that the optimal day for departure is near hatch (i.e., $c = 0$ days) because growth rates are higher at sea than at the colony. In reality, there is strong

evidence that the nidifugous pattern in *Synthliboramphus* is a response to heavy adult predation (Gaston 1992; Gaston and Jones 1998), but our model implies that selection pressure from energy gain does not counteract the selection pressure from adult predation. Third, if we assume that growth rates at the colony are similar to growth rates at sea—unlike members of Alcini that are single-prey loaders operating near an energy ceiling or members of *Synthliboramphus* that visit only infrequently at night and have two offspring to feed—then the model predicts that the optimal day for departure is near full growth (i.e., $c \approx 50$ days).

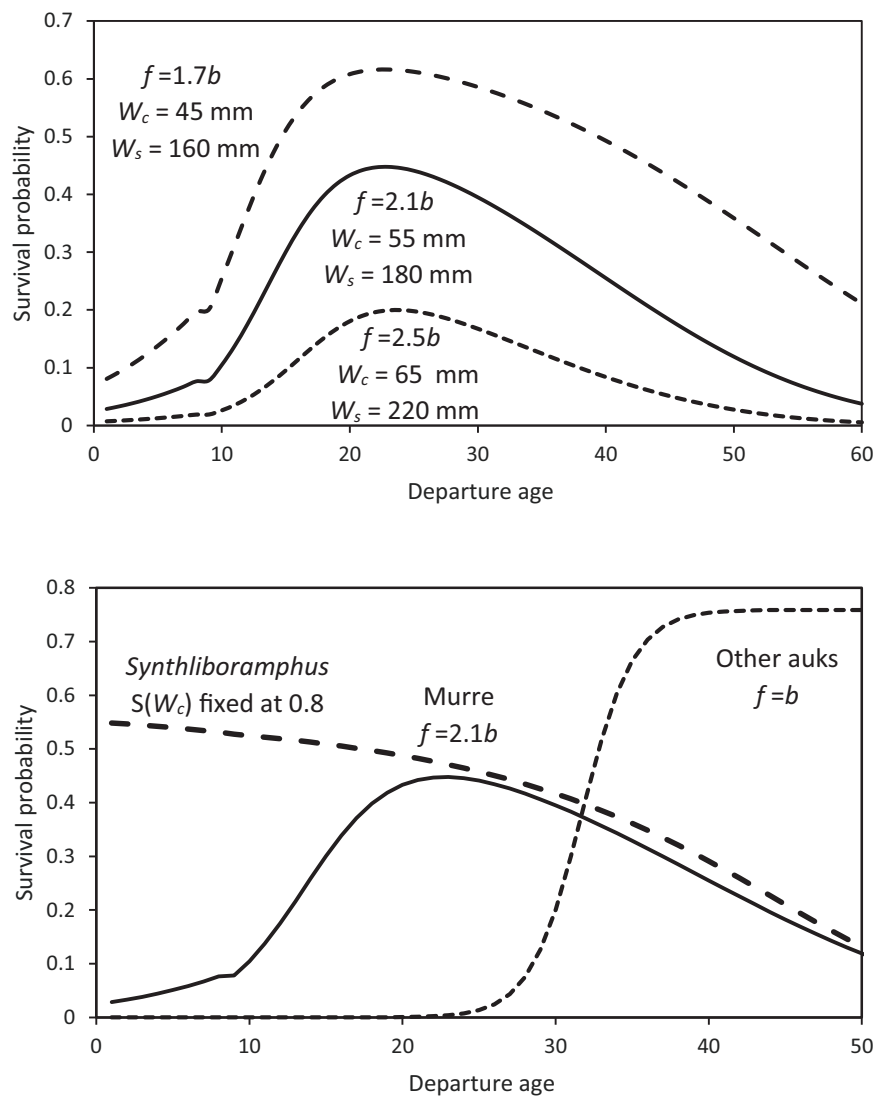


Figure 5: Model outputs showing postindependence survival probability (S) relative to colony departure day (c). *Top*, model output with predicted values (solid line) and values 20% lower than predicted values (dashed line) or 20% higher than predicted values (dotted lines). *Bottom*, comparison among different auk strategies. Shown are the default model from the top panel (solid line; Murre), model with survival during departure ($S(W_c) = 0.8$) being independent of wing length (dashed line; *Synthliboramphus*), and model with growth rate at sea being similar to the growth rate at the colony (dotted line; Other auks).

Discussion

We observed a sharp increase in energy intake—but no increase in mortality—following departure from the colony. For murres generally, and according to our model for auks generally, the duration of parental care was driven by variation in energy intake rather than mortality risk. Thus, for a famous natural history spectacle—the leap of tiny murre chicks off cliffs and down hundreds of meters to spend their following years far out at sea—we did not find any measurable foraging–predation risk trade-off, as previously modeled. Rather, the phenomenon appears to be driven by the limited ability of parents to provision their offspring at the colony compared with at sea. In contrast to the dominant paradigm that describes life-history transitions as the result of a trade-off between energy intake and mortality risk, our results imply that variation in energy intake alone may be enough to drive such transitions. Indeed, a review derived largely from studies on passerine birds concluded that variation in timing of independence was associated with levels of nest predation and ectoparasite-induced nestling mortality and that “availability of food does not influence nestling growth periods” (Mainwaring 2016, p. 1,422). Although perhaps more difficult to measure in the wild, we argue that variation in food availability likely strongly influences the evolution of nestling periods and, in particular, the duration of parental care (i.e., transition from dependence to independence) in a wide variety of animals.

Intersex and Interspecies Differences

On departure, ~21% of murre fathers lost their offspring, returned to the colony, and behaved similarly to females in terms of foraging. Those that did not lose their offspring foraged in low-quality patches, likely because they needed to stay close to the chick and could therefore access food only while swimming away from the colony. We presume that females—retaining the ability to search for food patches in flight—were able to identify and make use of higher-quality patches. Following an additional 1–2 weeks at the colony, females (and males without a chick) apparently flew in search of a high-quality patch and then started moulting and became flightless. Once at a patch, fathers apparently did not wander widely because the patch quality remained relatively constant. They spent more time foraging (diving) per day than females because they had to both make up for foraging in a low-quality patch and also feed the chick. As the chick grew, fathers spent more and more time foraging to meet the chick’s growing needs. Between ~20 and 35 days after departure, time spent foraging was approximately constant, presumably representing a ceiling on the amount of time a father could spend foraging. Time spent foraging then declined, likely because the chick was able to partially feed itself.

At ~37 days (thick-billed murres) or ~56 days (common murres) after departure, the chick apparently became independent, and the father (still flightless) spent much less time diving and swam to (or restricted foraging to) higher-quality patches, although still not as high as the female.

The consistent patterns in dive behavior across six winters, five colonies, and two species provide evidence that low patch quality and high dive rates is a consistent feature of paternal postdeparture care in murres. Despite being constrained by the flightless chick to forage in patches of low quality, males are still able to greatly increase energy delivery rates to their offspring by caring for them at sea. Although there was little difference in dive behavior among colonies (and therefore species), common murres spent longer raising their offspring than thick-billed murres. The difference suggests an advantage of migrating to the Arctic for reproduction. There was no difference in patch quality among colonies, implying that food availability was not noticeably higher in the Arctic. Rather, thick-billed murres raising their offspring in the Arctic spent more time per day diving (fig. 3, *middle*) because of longer daylight hours in August and most of September. Daylight constrains foraging opportunities in murres (Regular et al. 2011; Elliott and Gaston 2015) and Arctic seabirds generally (Grémillet et al. 2005; Daunt et al. 2007). If daylight rather than species-specific differences drives the trends we observed, then we would expect that common murres breeding at latitudes similar to thick-billed murres (i.e., Greenland, Norway) would show similar patterns to thick-billed murres at those latitudes.

The male-biased postdeparture parental care in murres contrasts with the female-biased parental care present in most animals (Paredes et al. 2006, 2008; Thaxter et al. 2009; Elliott et al. 2010; Burke et al. 2015). In some (Thaxter et al. 2009; Elliott et al. 2010) but not all (Burke et al. 2015) cases, female murres lose mass, expend more energy, and feed the offspring more before departure, allowing the male to maintain its reserves before the period of low energy availability at-sea. The divergent behavior of the two sexes after departure is much more pronounced than the divergence at any other time of the year (Burke et al. 2015), implying that males may somehow be more specialized or superior in their ability to forage at that time.

Addressing the Assumptions of Ydenberg’s Model

Our observations both refute and support aspects of Ydenberg’s model. In support of Ydenberg’s model, energy intake rate at sea by the chick was roughly twice that at the colony. In contrast to Ydenberg’s (1989) model, but as suggested by Gaston (1998) and as occurs in some of the parameter space in Ydenberg’s (2001) model, mortality at sea was lower than at the colony. Excluding departure, we estimated that mortality rate over 37 days of paternal care at sea was $<0.003 \text{ day}^{-1}$

(<1 in 13 over 30 days), lower than the mortality rate at the colony (~0.005 day⁻¹ from Ydenberg 1989; 0.0035 day⁻¹ from Gaston et al. 1983; 0.003 day⁻¹ from Gaston 1998) and well below the estimate provided by Ydenberg (1989) on the basis of survival to recruitment at the colony and assigning all mortality to the first winter. If we use the value of 56 days for the paternal care period of common murres, the at-sea daily mortality rate would be even lower. In short, we find little evidence that mortality at sea is higher than mortality at the colony during parental care.

If energy gain is higher at sea than at the colony, then why don't all other auks feed their offspring at sea? Parental constraints may account for variability in departure strategies. For instance, one important difference could be nest safety (Ydenberg 1989; Hipfner et al. 2001). Unlike cliff-nesting murres, most other auks nest in burrows and likely have a very low daily offspring predation rate at the colony, so there might be additional benefits in remaining longer at the colony. Nest safety may not be the only determinant, however; for example, razorbills—which nest in safer environments than murres—actually depart slightly earlier (Hipfner and Gaston 1999a, 1999b). Another difference could be the high cost of flight for murres and razorbills. Murres and razorbills are the largest auks (which permits them to avoid predation while nesting at open cliff sites) and consequently have the highest wing loadings in the family and exceptionally high flight costs (Thaxter et al. 2010; Elliott et al. 2013). Flight costs are so high that murres and razorbills are near an energy ceiling and are incapable of metabolizing more energy because they simply cannot assimilate and digest more food during the 12 h they are at sea each day (Hansen 2003; Elliott et al. 2014). By departing the colony with the offspring, they are suddenly free to forage 24 h day⁻¹ and—because dive costs are much lower than flight costs—require less energy for self-maintenance. Non-Alcini auks with lower wing loadings (lower flight costs) are multiple prey loaders (many fish per delivery) and are able to achieve more time flying per day and consequently feed their offspring more often while at the colony (although some are nocturnal visitors and therefore constrained to feed their offspring a maximum of only once per day). As chicks grow, they need more energy. The higher energy requirements may explain why the proportion of time spent diving increases with chick age (fig. 3). Murres and razorbills, near their energy ceiling, presumably cannot achieve the higher rates of energy gain needed to successfully raise large offspring at the colony.

Conclusions

A model based on growth rates at sea relative to those at colony explained much of the variation in auk parental care strategies. Duration of parental care was associated primarily with differences in energy intake between stages rather

than a foraging–predation risk trade-off. Similarly, cooperative breeders have a longer postfledging period than non-cooperative breeders (Langen 2000), implying that increased energy gain from helpers extends the duration of parental care in cooperative breeders. Perhaps differences in energy intake—more so than variation in safety—affect the age that altricial birds depart the nest, that parental mammalian carnivores begin to forage away from the den rather than suckling offspring, and that animals generally desert their offspring. We concluded that variation in energy gain alone was sufficient to drive variation in length of the transition from dependence to independence in certain birds, and we argue that energy intake—rather than mortality—needs to be taken into consideration more broadly as a potential driver for life-history transitions in animals.

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