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Breeding ecology of Kittlitz's Murrelets on Kodiak Island, Alaska

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ABSTRACT. Little is known about the breeding ecology of Kittlitz's Murrelets (*Brachyramphus brevirostris*), a species suspected to have experienced both local and regional population declines in recent years. We studied aspects of their breeding ecology on Kodiak Island, Alaska, to better understand this poorly described member of the family Alcidae. We found 53 nests of Kittlitz's Murrelets during our study (2008–2011) and placed nest cameras at 33 nests to collect data on parental nest attendance, nestling provisioning, and nest survival. Incubation shift exchanges by adults generally occurred either prior to sunrise or after sunset. Adults brooded nestlings for just one day after hatching and did not attend nests thereafter except during provisioning visits. Adults provisioned nestlings an average of 107 times during nestling periods, with a single fish delivered during each visit. Pacific sand lance (*Ammodytes hexapterus*), a high-lipid forage fish, accounted for 92% of fish delivered to nestlings. Nestlings grew rapidly, with a logistic growth rate constant (K) of 0.291, the highest rate yet documented among semiprecocial alcids. Young fledged an average of 25 d after hatching, when their body mass had reached an asymptote of 135.5 g, or 57% of adult body mass. Age at fledging and asymptotic nestling body mass (percent of adult mass) were low compared to other semiprecocial alcids. The mean number of young fledged per nest was 0.093, with 47% of nests predated, and nestlings dying prior to fledging at 21% of nests. The low number of parental provisioning visits, rapid nestling growth rates, and short nestling periods are consistent with adaptations to reduce the likelihood of nest predation and the energy expended by parents. The risk of nest predation and high energetic cost of breeding may make the reproductive success of Kittlitz's Murrelets more sensitive to declines in the availability and quality of their prey than most other alcids.

RESUMEN. **Ecología reproductiva del mérgulo *Brachyramphus brevirostris* en la isla Kodiak, Alaska**

Se sabe poco sobre la ecología de la reproducción del mérgulo *Brachyramphus brevirostris*, una especie de la cual se sospecha ha experimentado declines poblacionales locales y regionales en años recientes. Estudiamos aspectos de su biología reproductiva en la isla Kodiak, Alaska, para entender mejor a este integrante de la familia Alcidae escasamente descrita. Durante nuestro estudio (2008–2011), encontramos 53 nidos de este mérgulo y colectamos datos de cuidado parental en el nido, abasto a polluelos y sobrevivencia de nidos. Los intercambios de incubación de adultos generalmente ocurrieron antes del amanecer o después del ocaso. Los

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adultos criaron polluelos por un solo día después de la eclosión y no cuidaron los nidos en lo sucesivo, con excepción de las visitas de abastecimiento. Los adultos abastecían a los polluelos en promedio 107 veces durante su periodo en el nido, con un solo pez entregado durante cada visita. La especie *Ammodytes hexapterus*, una especie alimento alta en lípidos, significó el 92% de los peces que fueron entregados a los polluelos. Los polluelos crecieron rápidamente con una tasa logística de crecimiento constante (K) de 0.291, la tasa más alta documentada entre álcidos semiprecoces. En promedio, los polluelos abandonaron el nido 25 d después de la eclosión, cuando su masa corporal alcanzó una asíntota de 135.5 g o 57% de la masa corporal de los adultos. La edad de emancipación y la masa corporal asintótica de los polluelos (porcentaje de la masa corporal de los adultos) fueron bajos comparados con otros álcidos semiprecoces. La media de polluelos emancipados por nido fue 0.093, con 47% de los polluelos depredados y polluelos muriendo antes de la emancipación en el 21% de los nidos. El bajo número de visitas de abasto parental, la alta tasa de crecimiento de los polluelos y los periodos breves como polluelos en el nido son consistentes con adaptadores para reducir la probabilidad de depredación de nidos y la energía invertida por los padres. El riesgo de depredación y el alto costo energético de la reproducción en *Brachyramphus brevirostris* podría significar un éxito reproductivo muy sensible a declines en la disponibilidad y calidad de sus presas que en la mayoría de los otros álcidos.

Key words: *Brachyramphus brevirostris*, nestling provisioning, forage fish, growth rate, nest survival, predation, seabird

Kittlitz’s Murrelets (*Brachyramphus brevirostris*) are rare and enigmatic alcids of the North Pacific. *Brachyramphus* murrelets, including Marbled (*B. marmoratus*) and Long-billed (*B. perdix*) murrelets, are anomalous in the family Alcidae because their breeding plumage is cryptic and they nest non-colonially, usually in mainland areas, rather than colonially on small islands or sea cliffs typically inaccessible to terrestrial predators (Gaston and Jones 1998, Day et al. 2017). These traits suggest the importance of predation in the evolution of the breeding strategies of *Brachyramphus* murrelets compared to other alcids. However, few nests of Kittlitz’s Murrelets have been studied so many aspects of their breeding ecology remain unknown. Gaps in our knowledge of the breeding ecology of Kittlitz’s Murrelets are especially problematic because

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the species is suspected to have experienced both local and regional population declines in recent years (BirdLife International 2016), although considerable uncertainty exists regarding current trends in their populations (Day et al. 2017).

Among species in the family Alcidae, young vary in the age and body mass (relative to adult mass) when they leave nests, variation unparalleled in other avian families. Nestlings leave nests to go to sea as early as 1–2 d post-hatching, when as small as 15% of adult mass, when as old as 50 or more days post-hatching, and when as large as 100% of adult mass (Ydenberg 1989). Most alcid species, including *Brachyramphus* murrelets, are semiprecocial, with nestlings spending an extended period in nests and leaving nests capable of powered flight (Sealy 1973). Variability in juvenile life histories within the family Alcidae has been hypothesized to result from selection for optimal rates of nestling growth relative to parental investment (Ydenberg 1989). This hypothesis assumes that alcid nest sites are relatively safe from predators. However, the crypsis, exposed nest sites, and mainland nesting strategy of *Brachyramphus* murrelets, along with observed high rates of nest predation (Nelson and Hamer 1995a, Peery et al. 2004, Hébert et al. 2007, Kaler et al. 2009) suggest that their nest sites are at greater risk of predation than those of other alcids. Moreover, available information for *Brachyramphus* suggests that nestling periods are shorter than for most other semiprecocial alcids (Gaston and Jones 1998), which is expected in species with high rates of time-dependent mortality (e.g., predation and stochastic weather events) at nest sites (Lack 1968, Bosque and Bosque 1995).

Our primary objective was to obtain information on parental nest attendance, nestling provisioning, nestling growth and fledging, and nest survival of Kittlitz's Murrelets, aspects of their breeding ecology that are important for conservation and management, but are poorly described or absent in the published literature. We also sought to place aspects of the breeding ecology of Kittlitz's Murrelets within the context of their semiprecocial kin in the family Alcidae to better understand the adaptive factors that may underlie the atypical breeding ecology of this species and its two congeners. We focused on relationships among the semiprecocial Alcidae because of shared constraints on growth and development involved in leaving the nest by powered flight. Finally, we sought to determine if the atypical breeding strategy of Kittlitz's Murrelets could make them particularly sensitive to changes in the quality of fish provided to nestlings, a topic of interest given the dynamic and potentially changing ecosystem of the North

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Pacific (Anderson and Piatt 1999, Royer and Grosch 2006, Pinchuk et al. 2008, Sousa et al. 2016).

METHODS

Study area. Our study was conducted in mountainous terrain adjacent to the Sturgeon and Ayakulik rivers in southwestern Kodiak Island from 2008 to 2011 (Fig. 1). Kodiak Island lies in the northern Gulf of Alaska ~50 km south of mainland Alaska, and is the largest island in the Kodiak Archipelago (8975 km^2). Our study area included four sites collectively encompassing ~700 ha of alpine habitat dominated by broken-rock ground cover at elevations ranging from 80 to 471 m. The primary parent rock material in the study area is classified as ultramafic, a type of igneous rock containing high concentrations of heavy metals and limited nutrients, the combination of which inhibits the growth of most plants (Alexander et al. 2007). Expanses of ultramafic exposures provide broken-rock nesting habitat for Kittlitz's Murrelets at lower elevations than alpine areas elsewhere on Kodiak Island. Discrete patches of ultramafic rock in the study area were interspersed with and surrounded by upland and lowland tundra, forb meadows, and shrub communities variously dominated by Sitka alder (*Alnus viridis*), willows (*Salix* spp.), and crowberry (*Empetrum nigrum*). Although Kittlitz's Murrelets are often associated with glaciers during the breeding season (Day et al. 2017), the nearest glaciated terrain was ~70 km from our study area. Kodiak Island supports several native mammal and bird species that could predate Kittlitz's Murrelets and their nests, including short-tailed weasels (*Mustela erminea*), red foxes (*Vulpes vulpes*), brown bears (*Ursus arctos*), tundra voles (*Microtus oeconomus*), Common Ravens (*Corvus corax*), Bald Eagles (*Haliaeetus leucocephalus)*, Peregrine Falcons (*Falco peregrinus*), and Black-billed Magpies (*Pica hudsonia*).

Field methods. We located nests by systematically searching four sites on mountain slopes dominated by broken rock (see Lawonn et al. 2018 for additional details). We measured egg length and width (± 0.1 mm) with dial calipers and weighed eggs (± 0.5 g) with a 50-g spring scale. We estimated incubation stage by floating eggs in water, comparing their buoyancy to egg buoyancy benchmarks (Westerskov 1950, Rizzolo and Schmutz 2007) scaled to an assumed incubation period of 30 days (Day et al. 2017). We corrected for potential error associated with age estimates obtained from egg-floating using the method described in Lawonn

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(2012). If young were in the process of hatching when discovered, we either used nest-camera images (see below) to confirm hatching date or estimated hatch date based on the size of the pipped hole in the egg (based on estimates in Sealy 1970). To minimize the introduction of human scent, we wore latex or nitrile gloves when handling eggs, nestlings, or substrates near nests. We visited nests three times during the nestling period to collect data on nestling growth rates. We attempted to time our visits to coincide with nestling ages of 4–6 days post-hatching, 9–13 days post-hatching, and 19–21 days post-hatching. We used 100- or 500-g capacity spring scales to weigh nestlings (± 1 g). We measured straightened, flattened wing chords (± 1 mm) using a flexible metal ruler. Potential measurement error was minimized by training research assistants by the same person throughout our study.

We placed still-image, motion-triggered cameras (Reconyx Inc., Holmen, WI; Primos, PC 90, PC900) 1–3 m from a haphazardly selected subset of active nests (camera nests) to monitor nest activity. Cameras were painted to blend in with their surroundings prior to deployment, and fit with visors to reduce glare reflected from the lens and flash surfaces. We programmed cameras to photograph all motion-triggered events, and most were set to take one photo every 3 min, an interval selected to approximate the minimum time adult Kittlitz's Murrelets remain at nests when feeding young (J. Piatt and N. Naslund, unpubl. data). In 2011, three cameras were programmed to take photos at 1-min intervals to determine with greater precision the duration of nestling provisioning visits and incubation shift exchanges. We used preserved specimens of Pacific sand lance (*Ammodytes hexapterus*, a common forage fish), wing chord length of adult murrelets (125–140 mm, Day et al. 2017), and head-bill length of nestlings (45–55 mm, M. J. Lawonn, unpubl. data) as references for estimating the length of fish observed in images. We binned fish viewed in images into four size categories to facilitate analysis, including ≤ 8 cm, >8–12 cm, >12–16 cm, and >16 cm total length. We determined day of hatching from nest-camera images that showed eggshell fragments or frequent movements of an attending adult or nestling; we assumed hatching occurred at midnight on the day of hatching for calculating length of brooding and nestling periods. For non-camera nests, we estimated nestling age by comparing wing chords with a fitted line of wing chord as a function of age for known-age nestlings. We obtained data for sunrise, sunset, and civil twilight for the village of Karluk, Alaska (Astronomical Applications Department, U.S. Navy), the nearest location for which data were available; Karluk lies on a meridian ~8 km east of the center of our study area. We indexed

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nest activities to ambient light by calculating the difference between the time of nest events and sunrise or sunset, depending on which was closer in time. Visits before sunrise or after sunset were assigned positive values, and visits during daylight (after sunrise or before sunset) were assigned negative values.

Statistical analyses. We analyzed nestling growth rates using nonlinear mixed-effects models from the "nlme" package (Pinheiro et al. 2017) in the statistical program R (R Core Team 2011). Nonlinear mixed-effects models account for a lack of independence associated with repeated measurements by considering both individual-specific variation (random effects), and overall population-wide variation (fixed effects, Pinheiro and Bates 2000). Each nest was considered a grouping unit for random effects in models. To account for potential autocorrelation associated with repeated measures of the same nestling, we incorporated the autoregressive continuous correlation structure corCAR1 (Pinheiro and Bates 2000). We fit logistic growth curves of the form:

$$y = A/1 + e^{(-K(\text{age}-t_{i})),}$$

where A = asymptotic nestling mass, K = growth rate constant, and t_i = age (days post-hatch) at the inflection point of the growth curve. We used the logistic equation as a model for nestling growth in body mass (Sealy 1973). We followed Ricklefs (1983) and fit logistic equations to body mass as a function of nestling age and did not force the asymptote through adult body mass; we assumed mass at fledging was equivalent to asymptotic mass. We used the slope of the tangent at the inflection point as a measure of the maximum instantaneous growth rate. We analyzed food delivery rates across three years for nestlings that survived to at least 7 d post-hatching using generalized additive models (GAMs) from the "mgcv" package in R (Wood 2017). Our sample size for analysis of growth and provisioning rates was limited in all years except 2011, so we pooled nests across years for analyses. However, we provide annual summary statistics to illustrate possible inter-annual differences. We used Fisher's exact test to examine possible inter-annual differences in species composition and size of fish delivered to nestlings.

We estimated daily survival rates of nests using program MARK (White and Burnham 1999, Rotella et al. 2004). We developed a list of 20 *a priori* candidate models based on potential contributing factors to nest survival discussed in Rotella et al. (2004). Our candidate models incorporated overall nest age (days post-laying), nest stage (incubation vs. nestling), nestling age

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(days post-hatching), calendar date, year, site (*N* = 4), camera treatment (nest camera present or absent), and quadratic terms for nest age and calendar date. We evaluated candidate models in MARK using AIC*c*, and created a confidence set of models by including all models with AICc weights greater than 10% of the top model (Burnham and Anderson 2002). We used a model averaging function in MARK to estimate daily survival rates for our confidence set, and methods outlined in Burnham and Anderson (2002) to average coefficient estimates for models in our confidence set. Values are presented as means ± 1 SD.

RESULTS

Nest monitoring, nest initiation, and egg measurements. We discovered and monitored 53 active Kittlitz's Murrelet nests during 2008 (*N* = 5), 2009 (*N* = 13), 2010 (*N* = 15) and 2011 (*N* = 22), and placed motion-activated cameras near 33 of those nests. All nests contained a single egg (or nestling) and were located on the ground on slopes dominated by rocks of various sizes. The median estimated nest initiation (egg-laying) date across all years was 3 June (*N* = 53 nests; range = 18 May–17 July). The distribution of nest initiation dates was skewed toward later dates, with six nests initiated 30 days or more after 3 June. Average mass of fresh eggs (within 3 d of laying) across all years was 43.2 ± 3.2 g (*N* = 8, range = 39.0–47.5 g), ~18.3% of average range-wide adult mass of Kittlitz's Murrelets (236 g, Day et al. 2017). Mean egg length was 57.7 ± 2.2 mm (*N* = 43, range = 53.8–62.7 mm) and mean egg width was 38.2 ± 1.1 mm (*N* = 43, range = 36.3–40.8 mm).

Incubation and brooding. We reviewed images from 17 camera nests to determine the timing of incubation shift exchanges. Most exchanges were in the morning (*N* = 108, Fig. 2a), with just three in the evening (Fig. 2a). Morning incubation exchanges occurred an average of 44 min before sunrise (weighted SD = 28, *N* = 108 exchanges at 17 nests, range = -93–102 min; negative values denote time after sunrise/before sunset, see Methods); evening incubation exchanges occurred an average of 56 min before sunset (weighted SD = 123, *N* = 3 exchanges at three nests, range = -197–26 min). We determined intervals between incubation shifts at five nests where the two adults were distinguishable based on plumage. The overall weighted mean for the duration of incubation shifts was 28.5 h (weighted SD = 8.7, *N* = 64 observations at five nests, range = 21.3–48.6 h).

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Age estimates based on egg-floating were within 1 d of hatching for 10 of 18 nests with cameras, and within three days for 13 of 18 camera nests. The mean duration of continuous brooding periods (brooding hatchlings without a break > 2 h) was 31 ± 9.3 h (*N* = 15 nests, range = 14–47 h). At four nests, adults brooded young at least once following the cessation of continuous brooding; these discrete brooding bouts were brief (range = 4.5–6.8 h) and always occurred after food delivery. We did not observe adults attending nestlings other than when provisioning and brooding.

Nestling provisioning. We captured images of 1232 provisioning visits at 20 nests from 2009 to 2011. All deliveries consisted of a single fish. At three nests where cameras were deployed with 1-min photo intervals in 2011, only one of 199 deliveries involved an adult visiting a nest for less than 3 min. Therefore, we did not use a correction factor to estimate provisioning rates for the remainder of nests, where cameras were programmed to take photos at 3-min intervals. Only 24% of provisioning visits occurred before sunrise or after sunset. The distribution of provisioning visits was bimodal, with peaks occurring 42 min after sunrise and 18 min after sunset (Fig. 2b); 42% and 27% of deliveries occurred during the 4-h period centered on each of the morning and evening peaks, respectively. The remaining 31% of deliveries were made during intervals between morning and evening peak periods; 30% and 1% occurred during the daytime and night intervals, respectively (Fig. 2b). Provisioning adults remained at nests an average of 12.6 ± 6.9 min (*N* = 97 deliveries at 12 nests, range = 3.6–48.2 min). For the two nests with cameras programmed for photo intervals of 1-min, the mean time adults spent at nests after feeding young was 37 ± 15 sec (*N* = 19 deliveries, range = 13–75 sec).

Mean observed number of parental provisioning deliveries to nestlings monitored by camera during the entire nestling period was 85 in 2009 (*N* = 1), 81 in 2010 (*N* = 1), and 118 ± 25 deliveries in 2011 (*N* = 4, range = 99–154 deliveries). Statistical analysis of provisioning rates included data from 16 nestlings monitored in 2009 and 2010 (*N* = 2 each year) and 2011 (*N* = 12). The estimated peak in provisioning rates was on day 17 post-hatch, when nestlings were fed an estimated average of 4.8 times/day (95% CI: 4.5–5.2). Overall, parents made an average of 114 meal deliveries (95% CI: 104–124) to fledge a nestling during the 2009 to 2011 breeding seasons, based on model-predicted daily delivery rates and an observed average 25-d nestling period.

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Diet composition. We identified 998 (81%) of the fish delivered to nestlings (*N* = 1232 meals) either to species, i.e., Pacific sand lance, capelin (*Mallotus villosus*), and Pacific herring (*Clupea pallasii*), or family (i.e., Salmonidae). Identification of fish delivered during 234 provisioning visits (19%) was not possible due to poor image quality. We excluded unknown fish in a subsequent analysis of the proportion of different fish species delivered to nestlings. There was no significant inter-annual difference in the proportion of different fish species delivered to nestlings (*P* = 0.47, Fisher's exact test). From 2009 to 2011, fish delivered to nestlings included (by percent of deliveries) 91.7% Pacific sand lance, 7.6% capelin, 0.4% Pacific herring, and 0.2% salmonids. We found no inter-annual difference in the proportions of different size classes of fish delivered to nestlings (*P* = 0.10, Fisher's exact test). From 2009 to 2011, 71% (*N* = 838) of fish delivered to nestlings were 12–16 cm long, 27% (*N* = 324) were 8–12 cm long, and <2% were <8 cm or >16 cm long.

Nestling growth. We monitored growth of 15 nestlings from 2009 to 2011 (Fig. 4). For our model of growth rate, the estimate for the logistic growth rate constant (K) was 0.291 (95% CI = 0.232–0.387), the inflection point (I) of the fitted curve was 6.07 d (95% CI = 5.34–6.79), and the asymptote (A) was 135.5 g (95% CI = 125.7–145.3). Point estimates for parameters in the logistic growth model fit to all data on age-specific nestling body mass were similar to those that included only data from nestlings whose hatch dates were known (95% CIs: K = 0.222–0.384; I = 5.51–7.19; A = 127.1–148.2). The maximum instantaneous rate of growth, based on point estimates from the best-fit model, was 9.8 g/d at the inflection point of the fitted curve. The time required for a nestling to grow from 10% to 90% of asymptotic body mass ($t_{10–90}$, Ricklefs 1967) was 15.1 days.

Fledging. Mass (asymptotic body mass) of young at fledging from our growth model (135.5 g) was 57% of the range-wide average adult mass of Kittlitz's Murrelets (236 g, Day et al. 2017). Time and date of fledging were determined by cameras for seven nests, and by a scheduled nest visit <24 h prior to fledging at one nest (fledging was confirmed by a nest visit the following day). Mean age of young at fledging was 25 ± 2 d post-hatching across all years (*N* = 8 young, range = 22–28 d). Mean fledging age was 23 d in 2009 (*N* = 1 nest), 22 ± 0.6 d in 2010 (*N* = 3, range = 22–23 d), and 27 ± 1.3 d in 2011 (*N* = 4, range = 25–28 d). No fledging occurred at monitored nests in 2008. Six of seven young fledged an average of 25 ± 18 min (range = -1–42 min) either before sunrise (*N* = 3) or after sunset (*N* = 3). One nestling fledged

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3.7 h before sunrise. Median fledge date was 7 August (median ordinal day of year = 219, *N* = 8 nestlings, range = 204–244 day of year).

Nest fate and nesting success. Young fledged at nine of 53 nests, an apparent nest success rate of 17%. Predation was the main cause of nest failure. Predation events detected either on-camera or by visiting an active nest and finding it empty accounted for 47% (25 of 53 nests) of all nest fates. Of 25 predated nests, 18 (72%) and seven (28%) were predated during the incubation and nestling stages, respectively. Of 12 nests with cameras where predation was documented, 10 were predated by red foxes. We could not identify nest predators at two nests because the predator failed to trigger the camera. We found 11 nestlings dead in their nests, accounting for 21% of total nest fates from 2008 to 2011. Subsequent analysis of a sample of dead nestlings found in 2011 (*N* = 5) and 2012 (*N* = 3) revealed that exposure to saxitoxin, a biotoxin associated with paralytic shellfish poisoning, was a primary cause of chick mortality (Shearn-Bochsler et al. 2014). Seven of 52 eggs were abandoned during our study.

Our confidence set of nest survival models comprised four models within ~4 ΔAICc units of the best-fit model (Table 1). After averaging parameter estimates for our confidence set, the odds of nest survival were negatively associated with the year 2008 (*N* = 5 nests) and with the nestling period (95% CI for conditional odds ratios: 0.07–0.47 and 0.001–0.45, respectively). Assuming an average 55-d nesting period (incubation and nestling periods combined), overall survival rate for nests as derived from the confidence set of models averaged 0.076 (95% CI = 0.004–0.275) from 2008 to 2011. Camera deployment at nests had no significant effect on daily nest survival rate (95% CI for conditional odds ratio: 0.04–150), although the proportion of camera nests where nestlings fledged (0.21) was higher than the proportion of non-camera nests where nestlings fledged (0.10). We created a second confidence set of models without a camera term to derive a final estimate of nest survival rate. Based on this confidence set, the overall annual nest survival rate, or number of young fledged per pair (assuming no successful re-nesting attempts), was 0.093 (95% CI = 0.007–0.299).

DISCUSSION

Nest initiation, egg mass, and brooding period. Initiation of some nests as late as 4 to 6 weeks after the median nest initiation date suggests re-nesting attempts by failed breeders.

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Suspected re-nesting has been reported for Kittlitz's Murrelets (Day et al. 2017), and confirmed for Marbled Murrelets (Nelson 1997, Barbaree et al. 2014).

Mean egg mass of Kittlitz's Murrelets in our study (43.3 g) was slightly lower than that of five eggs at Agattu Island (46.6 g, Kaler et al. 2009). Taken together, the results of these two studies suggest that egg mass of Kittlitz's Murrelets, relative to adult body mass, is among the highest of the semiprecocial alcids (Table 2). Such large eggs are expected for precocial neonates (Starck and Ricklefs 1998b), and are consistent with the short brooding period and presumed rapid development of thermoregulatory ability observed in our study.

Nestlings on Kodiak Island were brooded by parents for a shorter period than nestlings of any other semiprecocial alcid except Marbled Murrelets. Such brief brooding periods are remarkable given that *Brachyramphus* murrelets use exposed nest sites, where nestling thermoregulatory costs are presumably high. Rapid development of thermoregulation may provide a net energetic benefit to the parent-offspring unit, allowing both adults to provision nestlings soon after hatching. Such a strategy increases the potential rate of food deliveries to the nestling, and eliminates the need for periods of parental fasting that accompany brooding.

Diet composition and rate and timing of provisioning. Most fish delivered to nestlings in our study were large (12–16 cm) Pacific sand lance and capelin, which are lipid-rich compared to many other potential forage fishes in the Gulf of Alaska (Van Pelt et al. 1997, Anthony et al. 2000, Iverson et al. 2002). Presumably as a result of feeding high-quality (large, lipid-rich) fish to their nestlings, adult Kittlitz's Murrelets on Kodiak Island made fewer provisioning trips during the nestling period than other fish-provisioning semiprecocial alcids, with the exception of congeneric Marbled Murrelets and nocturnal Rhinoceros Auklets (*Cerorhinca monocerata*; Fig. 5). Providing nestlings with high-quality meals seems adaptive in terms of both adult and nestling survival because it limits exposure of parents to potential predation associated with meal deliveries (especially from avian predators; Kissling et al. 2015, Day et al. 2017), and limits activity at nests that could attract predators (Martin et al. 2000). At the same time, such a strategy could reduce overall parental energy expenditure because the total energy required for raising young can be met with relatively few provisioning visits.

We found that ~30% of provisioning visits occurred during the daylight interval between morning and evening peaks of provisioning activity. Daytime nest visits presumably expose provisioning adults to increased risk of attack by avian predators and may increase the likelihood

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of nest detection by diurnal predators. Conversely, daytime provisioning may reduce the probability of nest detection by nocturnal predators such as red foxes that were commonly observed near murrelet nesting habitat (M. J. Lawonn, pers. observ.), and were responsible for the loss of some nests. Daytime provisioning of young has also been reported in Marbled Murrelets (Nelson and Hamer 1995b), but few data exist for comparison.

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Nestling growth and development. The growth rate constant (K) for nestling Kittlitz's Murrelets on Kodiak Island (0.291) was higher than that of nestlings at Agattu Island in the western Aleutians (K = 0.096, *N* = 4, Kaler et al. 2009), the only data available for comparison. This difference seems likely to reflect differences in the quality or quantity of food provided to nestlings at the two sites (USFWS 2013). The average duration of the nestling period at Kodiak Island (25 d) was shorter than that for two nestlings at Agattu Island (30 days, Kaler et al. 2009), but similar to nestling periods at single nests reported by Bailey (1973) and Naslund et al. (1994) at Cold Bay and Katchemak Bay, Alaska, respectively (estimated 24 d), and mean nestling periods in southeastern Alaska (23.7 days, *N* = 9 nests, USFWS 2013).

Average mass at fledging of young Kittlitz's Murrelets in our study was 57% of average adult mass, compared to 47% of adult body mass at fledging reported on Agattu Island (Kaler et al. 2009). The greater fledging mass of the comparatively fast-growing nestlings in our study is consistent with an observed inverse relationship between age and mass at fledging among many alcids (Ydenberg et al. 1995), and seems likely to be related to the apparent high quality of nestling diets in our study.

The growth rate constant for nestling Kittlitz's Murrelets in our study (K = 0.291) was the highest yet reported among semiprecocial alcids, whereas the asymptotic mass of nestlings was the lowest (57% adult mass). Associated with these two factors, our results suggest that Kittlitz's Murrelets have shorter nestling periods than other semiprecocial alcids. The rapid growth of chicks and abbreviated nestling periods of Kittlitz's Murrelets compared with their confamilials are consistent with an adaptive response to minimize the risk of time-dependent mortality associated with high-risk nest sites (Bosque and Bosque 1995). Rapid growth of nestlings may also have important energetic benefits for parents because faster growth rates appear to significantly reduce cumulative energy requirements of nestlings (Weathers 1992), translating to fewer overall provisioning visits required for fledging. Overall, by restricting energy demand at nests (i.e., one small, rapidly growing nestling with low asymptotic mass),

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Kittlitz's Murrelets on Kodiak Island were able to raise young that fledged quickly despite adults making relatively few provisioning visits during the nestling period.

Nest survival. Our estimate of nest success for Kittlitz's Murrelets was 0.093, a rate much lower than average nest survival rates for 18 other species of alcids (0.33–0.86, De Santo and Nelson 1995). This low rate seems insufficient to maintain a long-term murrelet population in our study area because, even with a generous assumption of 90% adult survival, nest success rates greater than 0.2 would be needed to maintain a stable population (Day and Nigro 2004). We acknowledge that our research activities could have increased the risk of predation risk for nests in our study (Piatt et al. 1990), but believe this is unlikely because of our limited number of nest visits, and because nests were not visited during incubation, when most nest predation occurred. Given low nest survival rates in our study, it is unclear whether the contemporary presence of Kittlitz's Murrelets in our study area is a result of periods marked by very high intrinsic productivity, immigration from more productive areas, or a combination of these two factors.

In our study, 13% of nests failed due to abandonment of eggs. Although possible reasons for this are unclear, we cannot discount our research activities as a contributing factor (Cairns 1980, Piatt et al. 1990, Rodway et al. 1996), even though we attempted to minimize the likelihood of abandonment by limiting nest visits to the post-hatch stage. Saxitoxin toxicity appears to have been a contributing factor for many of the 21% of nests with unexplained deaths of nestlings, but this seems likely to be a site-specific mortality factor rather than a population-wide phenomenon. Predation was the main cause of nest failure in our study, suggesting that Kittlitz's Murrelet nests in our study were under high risk of time-dependent mortality and that selective pressure may therefore favor short nestling periods to reduce this risk.

Conclusions. The high predation rates for Kittlitz's Murrelet nests observed at Kodiak Island and Agattu Island (Kaler et al. 2009) suggest that productivity may be constrained by nest predation in some areas. In contrast, non-*Brachyramphus* alcids are generally less exposed to predation pressure because they nest in areas that are usually inaccessible to ground-based predators, and benefit from the predator-swamping effect associated with colonial nesting (Gaston and Jones 1998). Thus, reduced availability of high-quality forage fish could disproportionately impair productivity of Kittlitz's Murrelets (and other *Brachyramphus* species) because a compensatory increase in the number of food deliveries along with slower chick growth (and a consequent lengthening of the nestling period) could increase exposure of

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nestlings and adults to predation risk. Forage quality may also impact Kittlitz's Murrelets via energetic constraints. Recent work suggests that the energy expenditure of adult Kittlitz's Murrelets relative to their metabolic capacity is high compared to other alcids, and may be close to their maximum physiological potential during breeding (Agness et al. 2013). Therefore, a reduction in forage quality could involve unusually high energetic costs for adult Kittlitz's Murrelets as a result of compensatory increases in the number of provisioning trips needed to raise young. Taken together, the potential effects of poor quality forage on both predation risk and parental energy demand suggest that Kittlitz's Murrelets may be especially sensitive to declines in forage quality compared to other alcids. Congeneric Marbled Murrelets have a similar breeding ecology and seem likely to experience similar energetic constraints during breeding. Such a sensitivity could be contributing to recent apparent declines in populations of Kittlitz's and Marbled murrelets in some areas in the Gulf of Alaska (Piatt et al. 2007, Day et al. 2017) that appear to coincide with shifts in the abundance of some lipid-rich forage fish in this region (Anderson and Piatt 1999).

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Table 1. Confidence set of nest survival models for Kittlitz's Murrelet nests on Kodiak Island, Alaska, 2008–2011.

Model	Number of parameters	ΔAIC*c*[f]	AIC*c* weights	Confidence set AIC*c* weights
Nest age[a] + nest stage[b] + nestling age[c] + camera[d] + year[e]	8	0.00	0.37948	0.44
Nest age + nest stage + nestling age + camera	5	0.06	0.36847	0.43
Nest age + nest stage + nestling age + year	7	3.50	0.06599	0.08
Nest age + nest age^2 + camera + year	7	4.13	0.04813	0.06

[a] Age of nest when discovered (days post-laying).

[b] Indicator variable for incubation (0) or nestling (1) periods.

[c] Age of nestlings; coded as an interaction term. Inclusion in models suggests difference in slope for survival of eggs vs. nestlings.

[d] Indicator variable for nests without camera (0) or with camera (1).

[e] Factor variable for study year. Reference group is 2011.

[f] Lowest AIC value for a confidence set model = 268.8

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Table 2. Estimates of reproductive parameters for 15 species of semiprecocial alcids (Family Alcidae)[a].

ID[b]	Species	Adult mass (g)	Mean egg mass (percent adult body mass)[c]	Brooding period (days)	Maximum fledging mass (percent adult mass)[d,e]	Maximum K (logistic)[e]	Minimum nestling period (days)[e]	Estimated mean number deliveries day^{-1}	Sources[f]
1	Dovekie	150–202	19	2–5	82	0.259	27	8	7, 11, 14, 25, 28, 30
2	Spectacled Guillemot	680	8	?	91	?	35	11.7	20, 22, 31
3	Black Guillemot	378–393	12	1–6	101	0.165	37	16.4	4, 8, 13, 14, 30
4	Pigeon Guillemot	450–507	12	3–7	98	0.171	35	18	9, 13, 30
KIMU	Kittlitz's Murrelet	212–244	19[g]	1[h]	57[g,h]	0.291[h]	23[h]	4.7[h]	6, 19, 23, 32, 35
MAMU	Marbled Murrelet	205–220	18	1–2	71	0.230[i]	27	3.2	15, 24, 29
7	Crested Auklet	260	14	1–6	94	0.197	33	3	10, 13, 17, 30
8	Least Auklet	82–87	22	5–7	108	0.244	29	3.5	3, 30
9	Whiskered Auklet	112–118	?	4–10	92	?	39	3	5, 13, 16
10	Cassin's Auklet	167–185	16	3–6	90	0.150	41	2	1, 13, 30
11	Parakeet Auklet	254–276	14	2–7	79	0.183	35	4	13, 18, 30

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12	Rhinoceros Auklet	491–569	16	4	73	0.126	48	2	2, 13, 30, 34
13	Tufted Puffin	721–829	12	1–4	78	0.153	38	4	27, 33
14	Horned Puffin	497–633	15	5–7	66	0.144	34	4	26, 33
15	Atlantic Puffin	405–480	15	6–7	75	0.181	38	5	11, 14, 21, 30

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[a] Estimates obtained from summary or primary literature and reflect summaries of average annual parameter estimates per study area, or summary estimates per study area when annual estimates unavailable.

[b] Scientific names (ID): (1) *Alle alle*, (2) *Cepphus carbo*, (3) *Cepphus grylle*, (4) *Cepphus columba*, (KIMU) *Brachyramphus brevirostris*, (MAMU) *Brachyramphus marmoratus*, (7) *Aethia cristatella*, (8) *Aethia pusilla*, (9) *Aethia pygmaea*, (10) *Ptychoramphus aleuticus*, (11) *Cyclorrhynchus psittacula*, (12) *Cerorhinca monocerata*, (13) *Fratercula cirrhata*, (14) *Fratercula corniculata*, and (15) *Fratercula arctica*.

[c] Average percent adult mass as reported; otherwise, calculated by dividing average egg mass by average location-specific pre-laying female adult mass or average adult mass if location-specific female mass was unavailable.

[d] Average percent adult mass as reported; otherwise, calculated by dividing average fledging or asymptotic nestling mass by average location-specific adult mass or species-specific adult mass if location-specific adult mass was unavailable.

[e] Intraspecific growth and developmental parameters vary considerably in the family Alcidae, complicating interspecific comparisons. We attempted to standardize comparisons by using parameters that achieve their presumed maxima (fledging mass, K) and minima (nestling period) under favorable conditions for nestling growth (Ricklefs 1968, Ydenberg et al. 1995).

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[f] Sources (and references therein): (1) Ainley et al. 2011, (2) Bertram et al. 1991, (3) Bond et al. 2013, (4) Butler and Buckley 2002, (5) Byrd and Williams 1993, (6) Day et al. 2017, (7) Evans 1981, (8) Ewins 1986, (9) Ewins 1993, (10) Fraser et al. 1999, (11) Gaston 1985, (12) Gaston and Dechesne 1996, (13) Gaston and Jones 1998, (14) Harris and Birkhead 1985, (15) Hirsch et al. 1981, (16) Hunter et al. 2002, (17) Jones 1993, (18) Jones et al. 2001, (19) Kaler et al. 2009, (20) Kitaysky 1994, (21) Lowther et al. 2002, (22) Minami et al. 1995, (23) Naslund et al. 1994, (24) Nelson 1997, (25) Norderhaug 1980, (26) Piatt and Kitaysky 2002a, (27) Piatt and Kitaysky 2002b, (28) Roby et al. 1981, (29) Simons 1980, (30) Starck and Ricklefs 1998a, (31) Thoresen 1984, (32) USFWS 2013, (33) Wehle 1983, (34) Wilson and Manuwal 1986, and (35) This study.

[g] Range-wide adult mass = 236 g (Day et al. 2017).

[h] This study.

[i] Only known growth data from two nests (Simons 1980, Hirsch et al. 1981).

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FIGURE LEGENDS

Fig. 1. Map of our study area on Kodiak Island, Alaska. Light-gray areas represent ultramafic outcrops dominated by broken rock. Ovals encompass sites where nest-searching occurred from 2008 to 2011. After Lawonn et al. 2018.

Fig. 2. (a) Timing of incubation shift exchanges by breeding pairs of Kittlitz's Murrelets (*N* = 17 nests), and (b) timing of provisioning visits to nests by adult Kittlitz's Murrelets (*N* = 20 nests) on Kodiak Island, Alaska, from 2009 to 2011 (Alaska Daylight Time). Solid lines represent sunrise and sunset; dashed lines represent civil twilight.

Fig. 3. Average meal delivery rates to nestling Kittlitz's Murrelets by adults on Kodiak Island, Alaska, during 2009 (*N* = 2 nests), 2010 (*N* = 2 nests), and 2011 (*N* = 12 nests). Dashed lines represent 95% confidence intervals. Points reflect data for individual nests; points jittered for clarity.

Fig. 4. Body mass of nestling Kittlitz's Murrelets as a function of age on Kodiak Island, Alaska, from 2009 to 2011. The curve represents a logistic model fitted to the data points.

Fig. 5. Number of provisioning visits required for successful fledging of young for 15 species of semiprecocial alcids, segregated by parental provisioning strategy. Number of provisioning visits determined by multiplying daily provisioning rates by the minimum duration of the nestling period. Provisioning rates for *Cepphus* species were based on a brood size of one nestling. Data and sources are provided in Table 2. Common names are: (1) Dovekie, (2) Spectacled Guillemot, (3) Black Guillemot, (4) Pigeon Guillemot, (KIMU) Kittlitz's Murrelet, (MAMU) Marbled Murrelet, (7) Crested Auklet, (8) Least Auklet, (9) Whiskered Auklet, (10) Cassin's Auklet, (11) Parakeet Auklet, (12) Rhinoceros Auklet, (13) Tufted Puffin, (14) Horned Puffin, and (15) Atlantic Puffin.

Fig. 6. Maximum fledging mass (percent of adult mass) as a function of minimum nestling period (days) for 15 species of semiprecocial alcids (after Fig. 1 in Ydenberg 1989, data from Table 2). Common names are: (1) Dovekie, (2) Spectacled Guillemot, (3) Black Guillemot, (4) Pigeon Guillemot, (7) Crested Auklet, (8) Least Auklet, (9) Whiskered Auklet, (10) Cassin's

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Auklet, (11) Parakeet Auklet, (12) Rhinoceros Auklet, (13) Tufted Puffin, (14) Horned Puffin, and (15) Atlantic Puffin.

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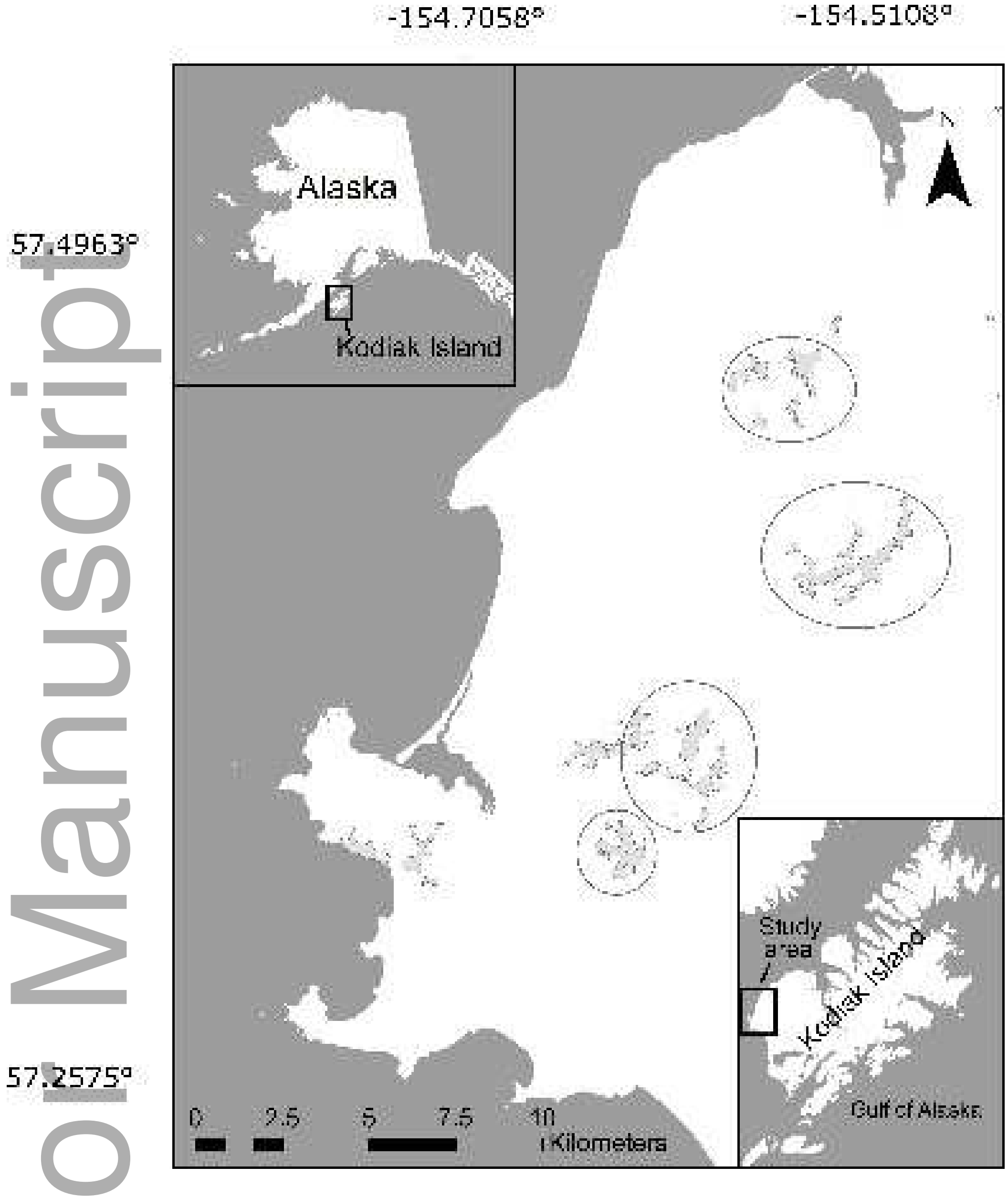

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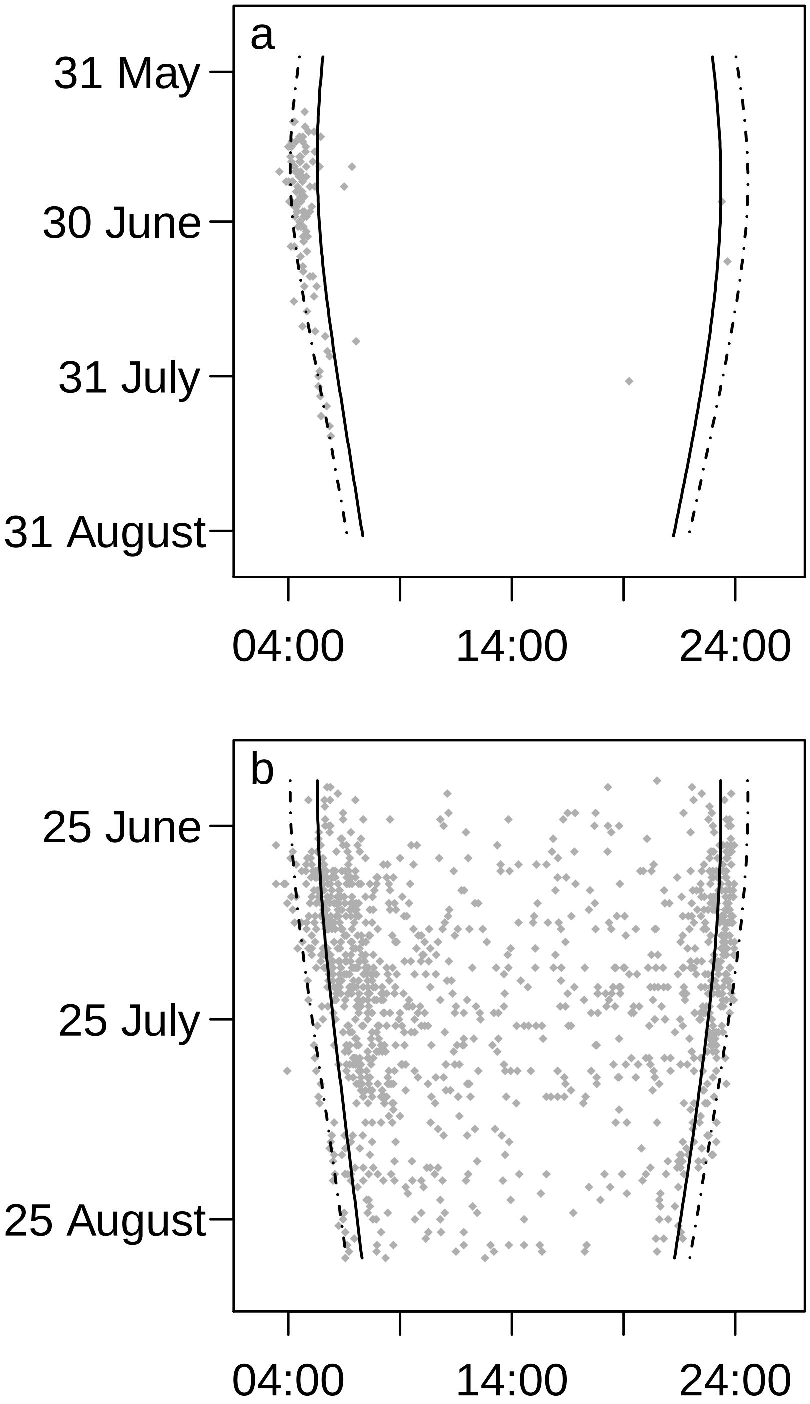

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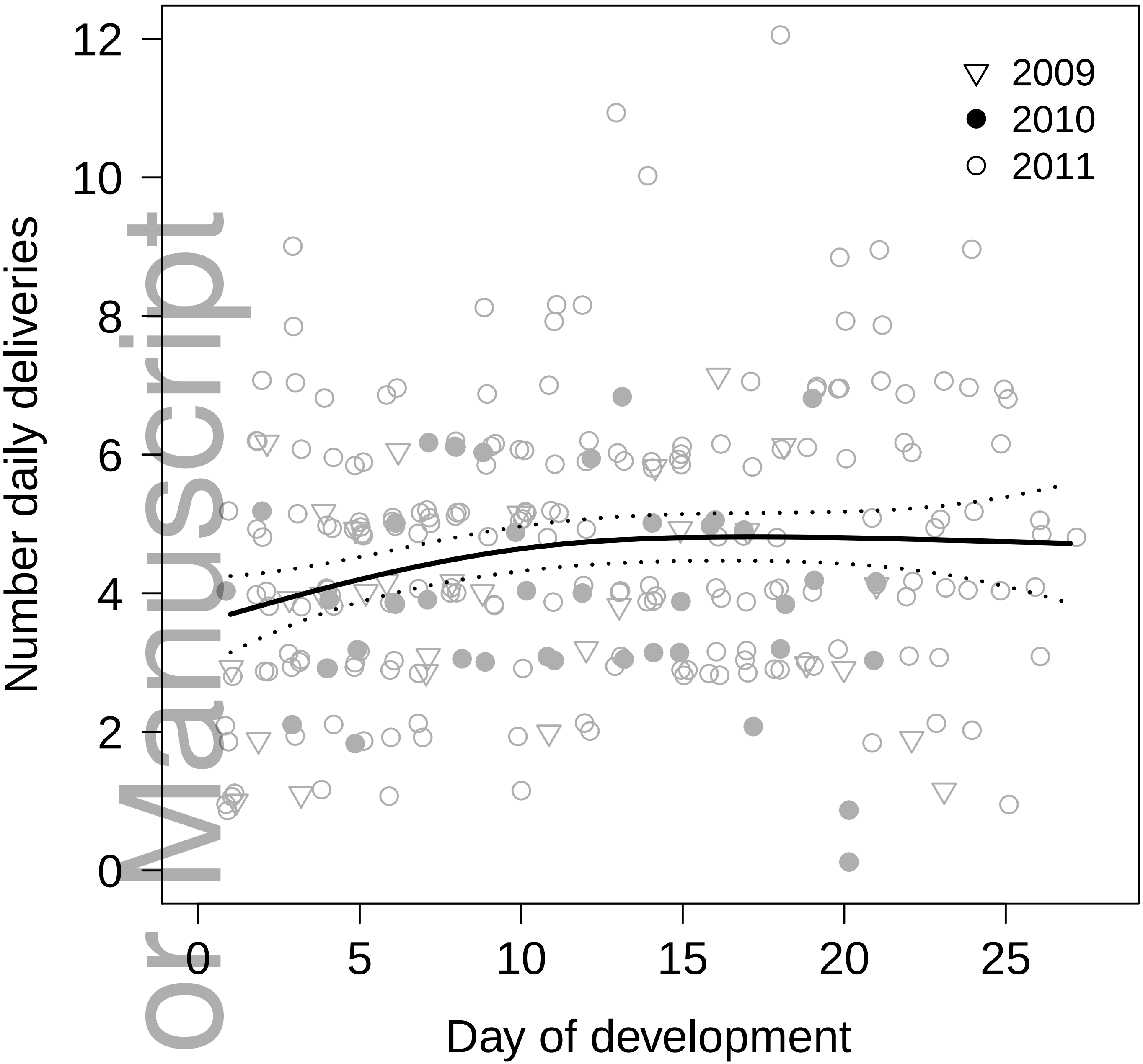

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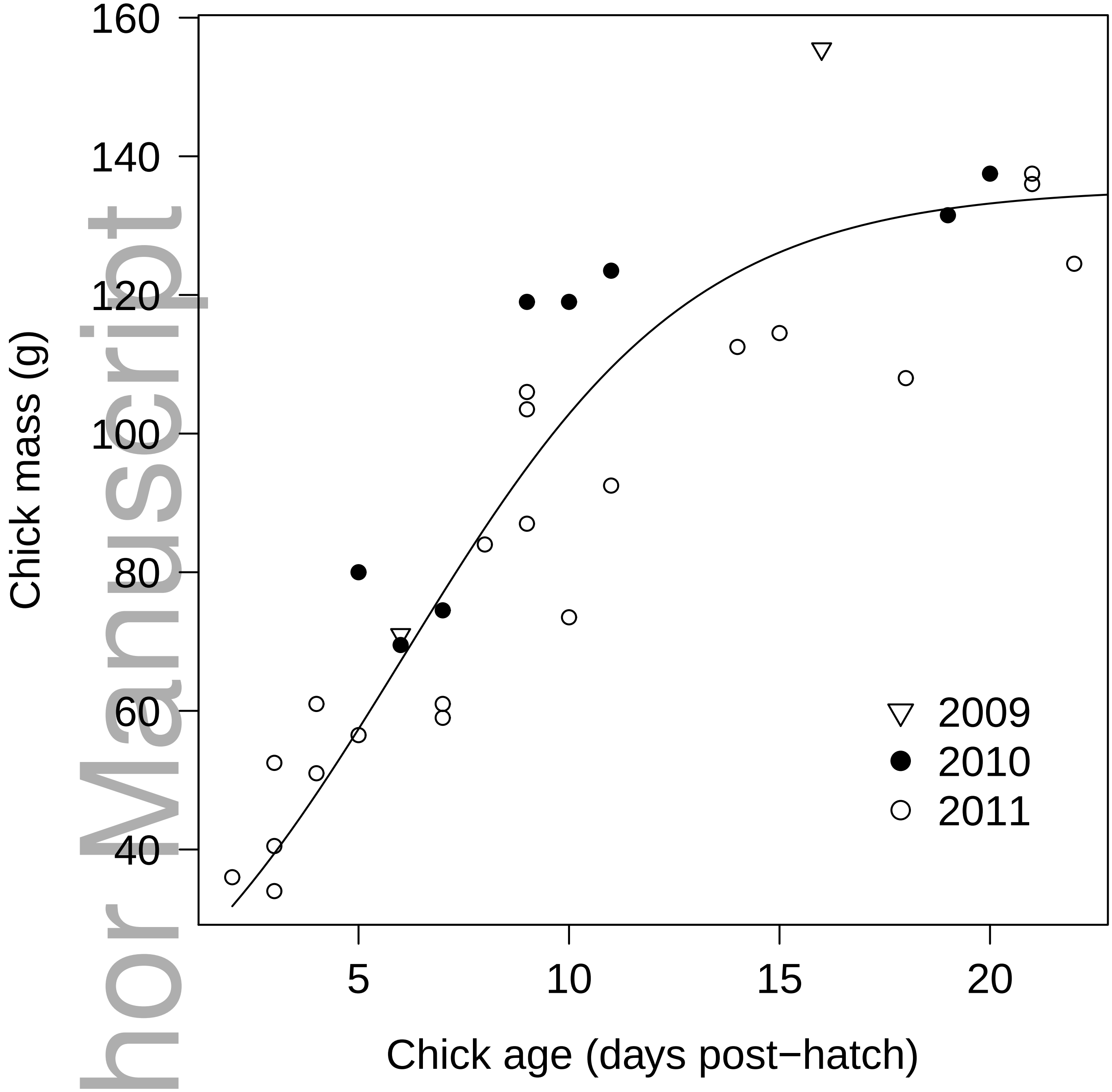

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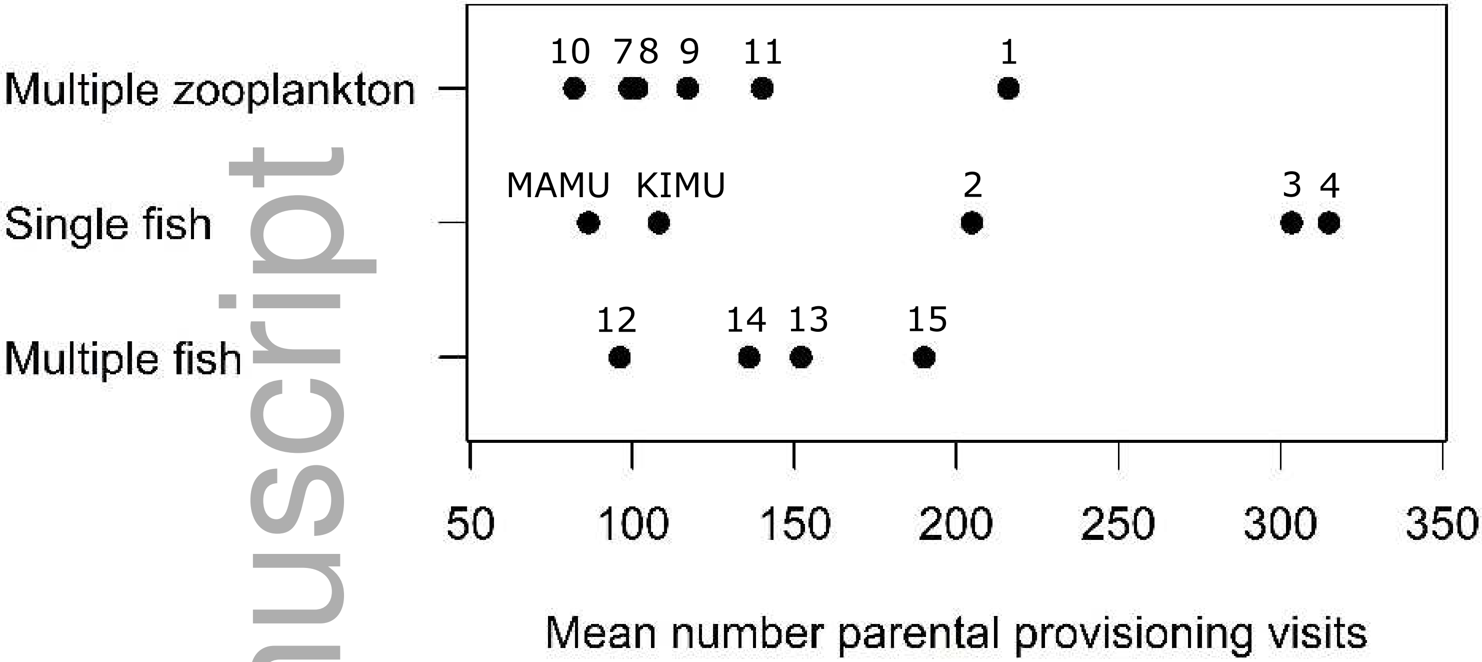

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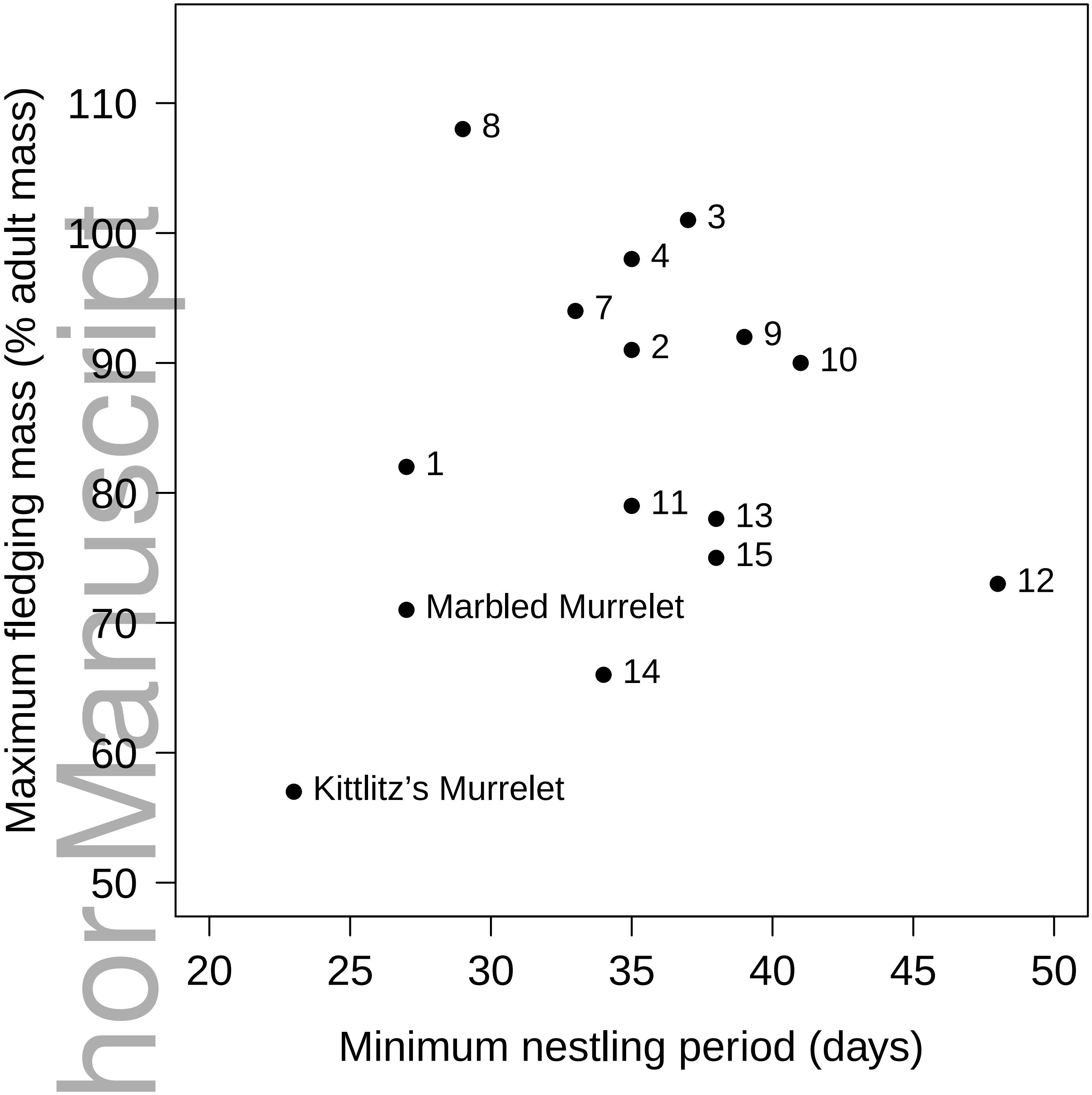

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