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RESEARCH ARTICLE

Turn-taking ceremonies in a colonial seabird: Does behavioral variation signal individual condition?

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ABSTRACT

In species with biparental care, pairs share a cooperative interest in offspring survival but may be in conflict over their relative investments, as reported in recent turn-taking studies of chick-provisioning birds. Turn-taking in Common Murres (*Uria aalge*) involves the foraging bird returning to the colony to provision the chick and the brooding parent departing. We examined whether Common Murres in poor condition had slower or more irregular turn-taking behavior, as has been documented in Common Murres equipped with geologgers. Irregularities include the brooding bird not trading parental roles with its returning mate or a bird returning to the colony without a fish. Irregular turn-taking sequences generally took longer than normal turn-taking sequences and differed in the rate and synchrony of allopreening, the main interactive behavior between mates. There was a delayed onset of allopreening when nest reliefs were protracted, whereas returners that did not bring a fish started allopreening sooner than either their brooding partners or other returners that brought a fish. Common Murres in better condition (higher body mass and lower lipid metabolite levels) left the colony sooner after their returning mates fed the chick compared to Common Murres in worse condition. Birds with higher chick-feeding rates brought fish back in more visits, which suggests that these were higher-quality birds. When birds vary in their turn-taking ceremonial behaviors, they may be negotiating by providing their partners with cues about their condition. Since Common Murres have long-term pair bonds and both parents are necessary to raise offspring, mates should respond to information from their partners if they can do so without compromising their own condition beyond a critical threshold.

Keywords: allopreening, bill fencing, negotiation, parental care, quality, turn-taking, *Uria aalge*

Cérémonies de prise de tour chez un oiseau de mer colonial : la variation dans le comportement est-elle un signe de la condition physique individuelle?

RÉSUMÉ

Chez les espèces dont les deux parents fournissent des soins aux jeunes, les couples partagent des intérêts coopératifs dans la survie des jeunes mais leurs investissements relatifs peuvent être en conflit, tel que dévoilé dans de récentes études sur la prise de tour lors du nourrissage des oisillons. La prise de tour chez *Uria aalge* implique le retour de l'oiseau en quête alimentaire vers la colonie pour nourrir l'oisillon et le départ du parent qui couvait. Nous avons examiné si les individus de cette espèce qui sont en mauvaise condition physique avaient un comportement plus lent ou plus irrégulier pour la prise de tour, tel que documenté chez des individus munis d'enregistreurs de données géographiques. Les irrégularités incluent que le parent couveur n'échange pas les rôles parentaux avec son partenaire qui revient ou l'oiseau revenant à la colonie sans poisson. Les séquences de prise de tour irrégulières étaient généralement plus longues que les séquences normales et différaient dans le taux et la synchronisation du lissage des plumes du partenaire, le principal comportement interactif entre les partenaires. Le début du lissage des plumes du partenaire était retardé lorsque les remplacements au nid étaient prolongés, alors que les oiseaux de retour au nid sans rapporter de poisson ont débuté le lissage des plumes du partenaire plus tôt que leur partenaire couveur et les oiseaux rapportant un poisson. Les individus en meilleure condition physique (plus grande masse corporelle et niveaux de métabolites lipidiques plus faibles) ont quitté la colonie plus tôt après que leur partenaire ait nourri l'oisillon à son retour, en comparaison des individus en mauvaise condition physique. Les oiseaux présentant des taux de nourrissage plus élevés rapportaient des poissons en plus de visites, ce qui suggère qu'il s'agissait d'oiseaux de meilleure qualité. Lorsque les oiseaux ont un comportement cérémoniel de prise de tour variable, il se pourrait qu'ils négocient en fournissant des indices sur leur condition physique à leur partenaire. Puisque le lien entre les partenaires est durable chez cette espèce et que les deux parents sont nécessaires pour élever la progéniture, les oiseaux

répondent aux renseignements fournis par leur partenaire s'ils peuvent le faire sans compromettre leur propre condition physique au-delà d'un seuil critique.

Mots-clés : escrime, lissage des plumes du partenaire, négociation, prise de tour, qualité, soins parentaux, *Uria aalge*

INTRODUCTION

Biparental care involves both cooperation and conflict (Trivers 1972, Griggio 2015). Individuals should behave in ways that maximize the survival of their offspring while minimizing energetic costs and mortality risk to themselves. Ultimately, a breeding pair shares a mutual interest in successfully raising offspring. However, parental conflict can occur when an individual's current body condition or future reproductive success is decreased because its partner's low investment has forced the individual to invest too heavily in the current reproductive effort (Houston et al. 2005, Saraux et al. 2011). Resolving this conflict may be particularly difficult in species with long-term pair bonds in which an individual's reproductive success depends on maintaining its partner's health as well as its own (Jones et al. 2002). Models of how pairs resolve this conflict have moved from one-time "sealed bids" (Houston and Davies 1985) to models that consider how partners negotiate turn-taking in real time in response to offspring state (Lessels and McNamera 2012) or the pattern of recent investment by both mates (Johnstone et al. 2014).

An important issue that arises in studies of parental turn-taking is how partners respond when one bird decreases its investment. The other bird may match its mate's decreased investment (e.g., Meade et al. 2011) or compensate for it (Kosztolányi et al. 2009), at least partially (Trnka and Grim 2013; meta-analysis: Harrison et al. 2009). Jones et al. (2002) suggested that compensation is critical for species in which both parents are necessary for successful reproduction, because an individual can compensate to prevent its mate's condition from deteriorating to the point of abandoning the breeding attempt. In seabirds with multiday incubation shifts, however, a bird may need to match its mate's longer trips in order to regain the considerable body mass it lost while the mate was away (e.g., Weimerskirch 1995, Dearborn 2001). Mass loss in these species is sometimes high enough that incubating birds abandon the egg (Chaurand and Weimerskirch 1994, Kato et al. 2008). Poor foraging conditions are associated with longer trip durations (Shoji et al. 2012, Berlincourt and Arnould 2015) and decreased reproductive success (Shoji et al. 2011). Shoji et al. (2015) traced the evolution of incubation-shift duration in seabirds and concluded that the ancestral pattern involved frequent diurnal exchanges. Longer shifts, generally accompanied by in-ground burrow nesting, evolved in some species as a means for individuals to have longer trip durations associated with foraging farther from the nesting colony. Shoji et al. (2015) suggested that a lower metabolism was one feature of this change so that birds could withstand not foraging for several days. One cost of this lower metabolism is that birds are less able to have complex interactions with conspecifics or predators.

Common Murres (*Uria aalge*) appear to be similar to the ancestral seabird described by Shoji et al. (2015), in that they have several nest reliefs each day and complex, interactive "nest relief ceremonies" when birds exchange duties. While there is a considerable seabird literature on whether one mate's trip duration affects its partner's subsequent foraging-trip length, very little is known about the actual nest-exchange process or ceremony and whether it involves a transfer of information between mates. In the colonial-nesting Common Murre, one parent always broods the chick, an antipredator strategy that ensures that the chick is not left alone on the open cliff. This constant chick attendance makes Common Murres ideal for studies of turn-taking ceremonies because parents are always present when their partners visit the nest and so they know how often the mate visits and whether or not the arriving mate has provisioned the chick. Turn-taking is initiated when the foraging individual returns to the colony and feeds a single fish to the chick. Usually, the returning bird then takes over brooding and the former brooder leaves the nest site to bathe and forage (Ricklefs 1983, Burger 1997), the entire interaction often taking several minutes. Variations in this sequence, here termed nest relief irregularities (approximately one-third of sequences; Storey et al. 2007), include the returner not bringing a fish or the brooding partner not giving up the chick or not leaving the colony, in which case the returning bird may depart to forage again.

Studies in which Common Murres carry data loggers may provide some insight into why individual birds might not adhere to strict turn-taking. Common Murres have the highest wing loading of any flying bird (Ainley et al. 2002), and the extra weight of carrying the loggers has been shown to affect their behavior and physiology. Common Murres carrying data loggers have higher corticosterone levels (Elliott et al. 2012), and they feed their chicks less often than controls or mates (Wanless et al. 1988, Hamel et al. 2004). They also have higher rates of irregularities in their turn-taking ceremonies than their mates or controls. Specifically, logger birds leave the colony less often than their mates or controls, and they bring fish back to the chick on a lower proportion of visits (Wanless et al. 1988, Hamel et al. 2004). It is possible that Common Murres

respond to data loggers as they would to natural variation in their condition.

Here, we examine whether birds that have longer turn-taking ceremonies or more frequent turn-taking irregularities have physiological markers that differ from other birds. The markers we use are body mass and level of beta-hydroxybutyrate (BUTY), a lipid metabolite associated with ongoing mass loss (Guglielmo et al. 2002, 2005). If turn-taking behavior is linked to condition, we can argue that birds in poor condition may provide information via their behavior. Mates may respond by compensating, that is, allowing the signaler more brooding time without provisioning the chick. For species in which individuals require extensive effort from their long-term partners to breed successfully, individuals should respond when their partners signal their poor condition; and they should attempt to compensate, if possible, without excessively compromising their own condition (Jones et al. 2002).

It may seem counterintuitive that a bird in poor condition should try to brood longer instead of leaving to forage. Several factors have likely selected for this nonobvious possibility. First, brooding is less energetically taxing than foraging: Resting metabolic rate is approximately half that during diving (Croll and McLaren 1993), and flight is energetically costly for alcids because of high wing-loading (Birt-Friesen et al. 1989, Gabrielsen 1996, Gaston 2004), so fewer colony departures would decrease total daily energy expenditure. Second, unlike some other seabirds with attendance bouts of several days (e.g., petrels and penguins), Common Murres switch roles 3–4 times day^{-1} on average (Wilhelm et al. 2008). Thus, even if brooders trade roles less often, they still have foraging opportunities. Finally, there are 2 distinct duties in Common Murre parental behavior during chick rearing: foraging and brooding. Divorce in Common Murres is associated with low chick-provisioning rates and, for the abandoned mate, it is followed by lengthy periods of remaining unpaired (Moody et al. 2005). It is possible that birds in poor condition opt to perform the less taxing parental role (i.e. brooding the chick), which might help them keep their mates even if their poor condition limits their foraging efficiency. According to Jones et al.'s (2002) model for bird species in which biparental care is necessary for successful reproduction, mates should push each other to do more work, but only if they can do so without risking either mate's condition dropping to the abandonment threshold. Thus, in species of this kind, mates need to respond to cues about their partner's condition and negotiate accordingly. One factor suggested to be important in how much compensation occurs is the quality and quantity of information that mates have about each other (Hinde 2006, Johnstone and Hinde 2006, Hinde and Kilner 2007), as well as individual differences in mate quality (van Dijk et al. 2012).

In addition to turn-taking irregularities, the present study also investigates what behaviors might be considered cues about partners' motivation to trade parental roles. One behavior involves delaying the exchange: Divorcing pairs had longer turn-taking sequences than pairs that remained together (Moody et al. 2005). Another common behavior during turn-taking sequences is allopreening, in which one bird preens the feathers of another bird (Harrison 1965). Allopreening has many hypothesized functions beyond hygiene, including social bonding (summarized in Lewis et al. 2007). High rates of allopreening and allopreening synchrony are associated with fewer divorces, higher compatibility, longer pair-bond maintenance, and higher reproductive success in birds (Spoon et al. 2006, Lewis et al. 2007, Gill 2012). Mutual synchrony in allopreening is seen mainly in mates, and less often in other social relationships (Gill 2012). Harrison (1965) suggested that allopreening functions to reduce aggression, and higher allopreening rates were indeed associated with less aggression in both Common Murre pairs (Lewis et al. 2007) and neighbors (Kober and Gaston 2003). Similarly, the bill fencing that is commonly seen when Common Murre pairs are together in the colony also appears to have aggressive components (Nørrevang 1958, Birkhead 1978), as it does in other bird species (Ellis 1966, Nelson 1978, Baptista and Atwood 1980).

The theoretical exploration by Jones et al. (2002) suggested that variation in behavior may provide important cues that a bird's mate is nearing the condition threshold at which it will abandon the breeding attempt and, thus, that mates should be sensitive to those behavioral cues. To investigate whether Common Murres negotiate parental duties with their mates, we first ask whether the various types of turn-taking ceremonies are associated with different patterns of interactive behavior within the pair. Are there any behavioral components of the ceremony—specifically, patterns of allopreening and bill fencing—that might provide birds with information about whether their mates will facilitate or delay the nest relief? Second, we test our hypothesis that behavioral characteristics of the turn-taking ceremony in Common Murres are related to the body condition of the brooder (as affected by geologgers in the studies described above). We test this hypothesis by examining whether, compared to individuals with predominantly short turn-taking sequences, individuals that prolong or prevent nest exchanges have lower body mass and higher rates of lipid metabolism (i.e. BUTY levels, as in Guglielmo et al. 2002, 2005).

METHODS

Study Site Location

The study was conducted from June 27 to August 2, 2009, on Gull Island (47°16′N, 52°46′W), Witless Bay Ecological

TABLE 1. Turn-taking and nest relief behavior patterns of Common Murres.

Term	Description of behavior
Total sequence time [a]	Total time that both individuals in the pair are at the nest site together, from the arrival of the foraging partner to the departure of either mate
Regular Nest Relief	Turn-taking sequence in which the returner comes in with a fish and the brooder leaves (exchange of brooding duties)
Multiple Nest Relief	Irregular turn-taking sequence in which the returner brings fish and there are multiple nest reliefs culminating in the brooder or the returner leaving
No Nest Relief	Irregular turn-taking sequence in which the returner brings fish and then leaves (no exchange of brooding duties)
No Fish sequence	Irregular turn-taking sequence in which the returner brings no fish and either the brooder leaves (nest relief) or the returner leaves (no exchange of brooding duties)
Latency to first nest relief [a]	Time from start of co-attendance to end of nest relief
Allopreening bout [a, b]	When an individual preens its partner; quantified as a single action beginning with the preener's bill contacting the partner and ending with bill withdrawal
Latency to allopreening [a, b]	Time from onset of co-attendance to when an individual starts to allopreen its partner
Bill fencing [a]	The touching of bills by both individuals in the pair
Latency to bill fencing [a]	Time from onset of co-attendance to when the birds in the pair begin bill fencing

[a] In seconds.
[b] These were quantified for the brooder and returner separately.

Reserve, Newfoundland, Canada, on 16 pairs of Common Murres with chicks. Two observers recorded behavior patterns from an observation blind located ~35 m from the study plot. The breeding pairs were distinguishable by the locations of their nest sites, by color bands on at least one individual of the pair, or by bridling (white eye-ring or spectacle and auricular groove behind eye morph seen in some Atlantic-coast Common Murres; Birkhead 1984, Ainley et al. 2002). Observations were made when chick ages were between 1 and 24 days (mean age = 11.0 ± 1.14 days). There were no systematic changes in nest relief ceremonies over the chick-rearing period. Typically, feeding rate—and thus visit rate—would increase over the ~3 wk chick-rearing period; however, 2009 was an exceptionally poor foraging year and feeding rates remained low throughout chick rearing.

Observers recorded individual behavior patterns (Table 1) using a camcorder, binoculars, and behavioral research software (Noldus Information Technology 2005, 2007) on a hand-held computer. A "turn-taking sequence" began when a returning bird ("returner") arrived at the nest site and joined its partner that was brooding the chick ("brooder") and ended when one of the pair members departed.

A Canon VIXIA HF20 Dual Flash Memory camcorder was used to record up to 6 hr day^{-1} of intra-pair interactions over 35 days. The camcorder's zooming capability enabled us to record 1 of 5 groups of pairs in a single frame (not the entire study plot). Therefore, multiple sequences could be recorded at one time at adjacent nest sites. We also used a Noldus Information Technology Pocket Observer 2.0 software program on a PSION Teklogix Workabout Pro Hand-Held computer (C version) in order to maximize the number of nest sites with recorded sequences.

Data Extraction

The camcorder recording format was converted from the Advanced Video Codec High Definition (AVCHD; file extension of *.mts) to a video file format (file extension of *.m4v) to be compatible with the program logger.app (Earle 2007; an event recorder designed for recordings played in QuickTime that was used for coding). In total, 248 behavioral sequences divided into 231 "Fish" and 17 "No Fish" sequence types (62.04 hr) were recorded with the camcorder. Observations on the Noldus device were extracted with Observer XT (Noldus Information Technology 2007). In total, 65 behavioral sequences divided into 52 "Fish" and 13 "No Fish" sequence types (17.38 hr) were recorded with the Noldus. These behaviors were noted on the Noldus as either single or grouped actions representing bouts of allopreening (1–3, 3–6, and 7–10 bouts) and were averaged as 2, 5, and 8 bouts, respectively, for comparison with the camcorder data. Duration measures were similar for both recording techniques. Allopreening rates were lower with the Noldus than with video analysis for sequences that were recorded both ways ($n = 7$ sequences). Since we obtained a high proportion of No Fish turn-taking sequences with the Noldus, for which behavioral frequencies were generally higher, this difference between recording systems made our results more conservative than if all sequences had been recorded with video. Latency to the onset of allopreening did not differ with the 2 recording methods, and the pattern for latency results is similar to that for allopreening rate. One observer (L.S.T.) performed all video extraction and coding.

Unpublished data from all-day watches in an adjacent Common Murre colony indicated that feeding frequencies were higher in the morning than later in the day (consistent with Harris and Wanless 1985, Burger and

Piatt 1990), and nest relief sequences involving the returner bringing a fish were shorter in the morning than in the afternoon. Thus, most of the data are from this morning period. The exception is the irregular type of nest relief sequence in which the returner does not bring a fish. Both morning and afternoon data were used in these cases, because the nest relief behaviors did not differ statistically by time of day and the number of total No Fish sequences was small ($n = 30$). The 4 turn-taking sequence types as well as definitions of allopreening and bill fencing are presented in Table 1. These Common Murres had no sex-specific brooding patterns, unlike Thick-billed Murres (*Uria lomvia*) in some colonies where brooding is primarily conducted by males at night and by females during the day (Paredes et al. 2006).

Body Condition Indicators

We used a 7 m noosepole to capture focal birds on 1 of 2 days in the middle of the chick-rearing period (success: 14 of 32 focal birds). Captured Common Murres were weighed and a 2.5 mL blood sample was taken. Color bands and metal leg bands were attached so that we could recognize pair members. We extracted serum from the blood samples to measure BUTY levels. Serum samples were analyzed for BUTY concentration using a microplate spectophotometer (Biotech Powerwave XS, Fisher Scientific, Nepean, Ontario, Canada) and a kinetic endpoint assay (kit E0907979, R-Biopharm, Marshall, Michigan, USA), as described in Guglielmo et al. (2002, 2005). Blood spots were also analyzed for corticosterone levels (as in Doody et al. 2008, Rector et al. 2012), but there was no relationship between corticosterone and the other physiological or behavioral measures, so there will be no further mention of that hormone here.

Body mass was used as the condition indicator because it provides essentially the same information as body condition indices in alcid seabirds. Because variation in mass reflects changes in lipid storage (Jacobs et al. 2012), it is increasingly used as a measure of body condition in these birds (e.g., Gaston and Hipfner 2006, Elliott et al. 2010, Rector et al. 2012, A. E. Storey et al. personal communication).

In addition to the 14 birds captured in 2009, we also used an inter-year comparison to estimate the body mass of some birds not captured in that year. Four birds had been measured in both 2007 and 2009. The average difference between the body conditions of these 4 birds was applied to the birds captured only in 2007 so that an "adjusted 2009" body mass could be calculated for the 7 focal birds captured only in 2007, making a total of 21 birds with actual or estimated body mass. Birds differed in the 2 yr by <4% (i.e. they were 33 g lighter, on average, in 2009 for birds with a mean mass of 980 g). Since the average difference between high- and low-quality birds was

~6%, the use of 2007 data to estimate mass in 2009 was deemed acceptable. The correlation was the same for total sequence time and the adjusted mass in 21 birds ($r = -0.633$, $P = 0.002$) and for the 14 birds actually measured ($r = -0.639$, $P = 0.014$), which supports our use of the adjusted values. Using the adjusted mass values allowed us to create 8 pairs in which one of the partners could be distinguished as being in better body condition than the other (called "matched pairs" below).

Sex Determination

DNA was extracted from blood spot cards using DNeasy Blood and Tissue Kits (Qiagen, Toronto, Canada), and individuals were sexed using a molecular method based on CHD (chromodomain helicase DNA; Fridolfsson and Ellegren 1999). Highly conserved primers (2550F and 2718R) were used. Females were identified by 2 fragments (CHD1W and CHD1Z); males were identified by 1 fragment (CHD1Z), following polymerase chain reactions and agarose electrophoresis.

Statistical Analyses

Linear mixed-effects models (LMMs) were constructed to examine whether behaviors exhibited during nest relief sequences were significantly influenced by Common Murre sex and type of sequence, as well as their interaction (Table 1). Because these data involved repeated measures and we had no prior knowledge of what the model covariance structures should be, we evaluated covariance structures via likelihood ratio tests using REML estimation for repeated effects (with subjects nested within site) in accordance with West et al. (2007). In brief, this approach involves evaluation of the −2 restricted log-likelihood (−2RLL) information criterion for models in which the covariance structure is systematically changed; the difference between the two −2RLL values approximates a chi-square distribution with degrees of freedom equal to the difference of the degrees of freedom for the 2 models. If the chi-square value is significant, this indicates that one model is an improvement over the other and should be selected.

Nest relief type was a categorical variable, with 7 of 16 pairs demonstrating all 4 types of nest relief (see Table 1); variation across pairs was due to the stochastic nature of "catching" nest reliefs at each site on the camera. Likely as a consequence of these missing observations in 3 of the 4 nest relief categories (all irregular turn-taking sequences), full random-effects models (i.e. those including random intercepts and random slopes) failed to converge for any dependent measure evaluated. Thus, our approach—following Barr et al.'s (2013) "fallback strategy"—was to use a data-driven approach and build mixed models starting with only fixed effects, and then to evaluate whether the addition of a single random intercept (nest

site) improved the model significantly, again examined via −2RLL testing. Further attempts to integrate random slopes (both with and without random intercepts) were made, but slopes were ultimately excluded in all models due to failure of the models to converge when they were included as random effects. We report the results of the best model for each behavior. This data-driven approach to LMMs is potentially anti-conservative (Barr et al. 2013). However, given that these data analyses are largely exploratory, we consider the approach both justified and likely to provide outcomes on which future hypothesis testing can build. Significant ANOVA results were followed by LSD post hoc tests.

Although our analyses depend primarily on LMMs, linear regression was used to show which variables best predicted the total time for the turn-taking sequences ($n = 32$ for behavioral analysis; $n = 21$ for adjusted body mass; $n = 14$ for body mass and BUTY level). For the sequence closest to capture for the birds with estimated body mass, we used the sequence that fell closest to the middle of the interval between the 2 dates that the actual captures took place in the middle of the chick-rearing period. Due to relatively small sample sizes, only 2 predictors were included in the analyses involving body condition measures. The model with the highest adjusted R^2 value was accepted, and other close candidate models are provided for comparison. There were also cases for which we compared returners and brooders in the same pairs (e.g., the matched pairs); we used paired t-tests for these analyses. To avoid pseudoreplication, we used the average for each behavior for each individual in these analyses.

All statistical analyses were conducted using SPSS 23.0 (IBM, Armonk, New York, USA) with a significance level of $\alpha = 0.05$. Results are presented as mean $\pm$ SE unless otherwise specified.

RESULTS

Frequency of Different Types of Nest Relief Ceremonies

Analyses were conducted on 198 video-recorded nest reliefs for 32 birds at 16 nest sites. All pairs showed both Regular Nest Relief (frequency site^{-1} = 6.44 ± 0.72; range: 2–10) and at least one irregular nest relief type (combined frequency site^{-1} = 5.94 ± 0.93; range: 1–13). The total number of nest reliefs observed at each site ranged from 4 to 23, which was likely a function of camera position (see above), as well as pair activity during the time when particular sites were recorded. With the exception of the irregular nest relief type No Fish sequence, only morning nest reliefs were evaluated, because this was the period of highest chick-feeding frequency and, hence, nest relief opportunities. Proportions of nest relief types for the morning were as follows: Regular Nest Relief, 103/198
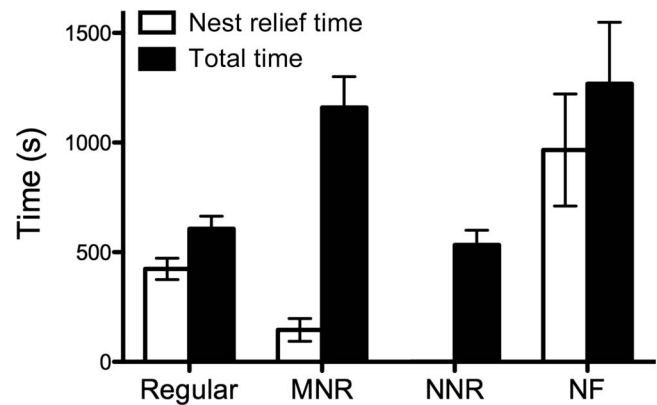

FIGURE 1. Total co-attendance time and time to the first nest relief (means ± SE) in our study pairs of Common Murres for the 4 turn-taking sequence types: Regular = Regular Nest Relief, MNR = Multiple Nest Reliefs, NNR = No Nest Relief (returner rather than brooder departs), and NF = No Fish.

(52%); No Nest Relief, 42/198 (21%); Multiple Nest Reliefs, 23/198 (12%). There were 30/313 (9.6%) No Fish sequences recorded across morning and afternoon sessions. Multiple nest sequences consisted of either 2 ($n = 13$) or 3 ($n = 10$) brooding exchanges before one partner left the site. In the cases of 2 exchanges, the original returner left the colony; with 3 exchanges, the original brooder left.

Are the Different Types of Nest Relief Ceremonies Associated with Different Patterns of Interactive Behavior?

Time together and latency to exchange duties. The total sequence time differed significantly in the various types of nest reliefs ($F = 10.31$, df = 3 and 94.82, $P < 0.001$; Figures 1 and 2). Pairs spent less time together in Regular Nest Relief and No Nest Relief sequences than they did for Multiple Nest Reliefs (LSD post hoc tests: $P = 0.004$ and 0.006, respectively) and No Fish sequences (both $P < 0.001$; Figures 1 and 2). Mean time together in No Nest Relief sequences did not differ from Regular Nest Relief. There was no sex difference and no interaction.

Latency to the first nest relief (exchange of brooding duties) from the time the incoming bird arrived at the nest site varied significantly with nest relief type (excluding the No Nest Relief scenarios, which had no exchanges; $F = 12.88$, df = 2 and 139.50, $P < 0.001$). All 3 nest relief scenarios differed significantly from each other for latency to nest relief (or to first nest relief in the case of Multiple Nest Relief scenarios). Latency to first exchange of duties was the shortest in Multiple Nest Reliefs (144.82 ± 119.34 s), followed by Regular Nest Relief (410.56 ± 60.99 s), and was longest in No Fish sequences (950.00 ± 119.59 s). Thus, brooders appear to resist nest relief when the partner does not bring a fish.
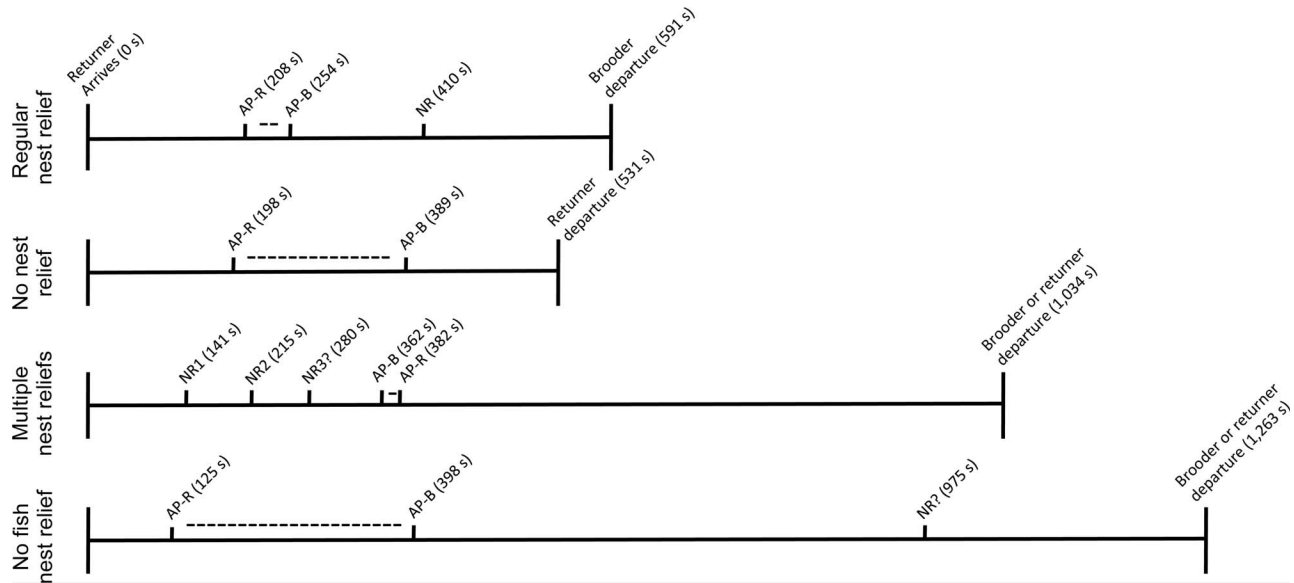
FIGURE 2. A scale illustration of the timing of events (in seconds) during the 4 types of nest relief sequences in our study pairs of Common Murres, with mean time of nest relief (NR) and mean latency to allopreening in brooders (AP-B) and returners (AP-R). "NR" with a number refers to the sequence of nest reliefs in a multiple nest relief sequence, and "NR?" refers to sequences in which either the brooder or the returner leaves. Dashed line shows length of interval between mean onset of allopreening by the returner and mean onset of allopreening by the brooder.

Allopreening rate. The rate of allopreening by the returning bird differed by the type of turn-taking sequence (overall $F = 4.28$, df $= 3$ and 119.09, $P = 0.007$; Table 2). Specifically, birds arriving without a fish for the chick allopreened their brooding partner at a significantly higher rate than they did in all other nest relief types (Table 2). There was no significant interaction between sex and nest relief type. Rates of allopreening by brooders after their mates returned also differed by nest relief type. Rates were significantly lower in No Nest Relief sequences than in any other nest relief types (overall $F = 2.97$, df $= 3$ and 74.24, $P = 0.037$; Table 2).

Latency to allopreen. Latency to allopreen by Common Murres arriving at the nest site differed significantly in the various turn-taking sequence types ($F = 5.62$, df $= 3$ and 189.2, $P = 0.001$; Figures 2 and 3). Common Murres engaged in Multiple Nest Reliefs started allopreening significantly later than birds in any other nest relief type (all $P < 0.001$). Latency to allopreen by the brooder also differed significantly by nest relief type ($F = 3.46$, df $= 3$ and 108.25, $P = 0.019$). Specifically, compared to Regular Nest Relief, brooders delayed allopreening in No Nest Relief

sequences in which the recently arrived partner departed ($P = 0.005$; Figures 2 and 3). As with all analyses in this study, there were no significant sex differences.

Allopreening symmetry. Returners in both No Fish and No Nest Relief sequences started allopreening sooner than their brooding mates (within-pair analyses: $t = -2.43$, df $= 15$, $P = 0.028$; $t = 4.34$, df $= 13$, $P = 0.001$, respectively; Figures 2 and 3). These results are consistent with the results for allopreening rates and latencies; compared to the other sequence types, brooders started allopreening latest in the No Nest Relief sequences. There was no difference between mates in the latency to allopreen in either Regular Nest Relief or Multiple Nest Relief sequences. Although these 2 turn-taking sequences had symmetrical allopreening patterns, they differed in the timing of the onset of allopreening: pairs started allopreening before the nest relief in Regular Nest Relief but typically did not start until after at least one nest relief in the Multiple Nest Relief sequences (Figure 2).

Bill fence rate and latency. Bill fencing was observed in 79% (156/198) of nest reliefs. Bill fence rate and latency to

TABLE 2. Mean ($\pm$ SE) allopreening rates of returners and brooders, in our study pairs of Common Murres, for 4 types of turn-taking sequences (nest relief $=$ NR). Values in bold are significantly different from all other values in the same row. The same letter for returner and brooder indicates the nest relief types that had asymmetrical allopreening rates within pairs.

	Regular NR	No NR	Multiple NR	No Fish
Returner	0.012 ± 0.002	0.019 ± 0.003 [a]	0.011 ± 0.003	**0.024 ± 0.004** [b]
Brooder	0.012 ± 0.002	**0.004 ± 0.003** [a]	0.014 ± 0.003	0.012 ± 0.003 [b]
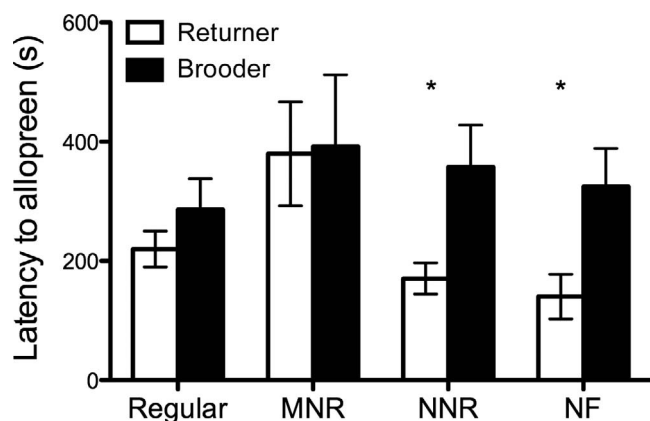
FIGURE 3. Mean allopreening latency, in our study pairs of Common Murres, by returners and brooders of the same pairs in the 4 sequence types: Regular = regular nest relief, MNR = Multiple Nest Reliefs, NNR = No Nest Relief (returner rather than brooder departs), and NF = No Fish.

bill fencing did not differ with type of turn-taking sequence or with average total sequence time. There was a higher mean frequency of bill fencing in the Multiple Nest Reliefs in which the brooder finally left after the third nest relief (14.9 ± 3.4 bouts) compared to when the returner left after the second nest relief (5.0 ± 1.6 bouts, $t = 2.79$, df = 11.54, $P = 0.025$, $n = 22$; all individuals are in each group only once).

Are the Behavioral Components of Nest Relief Ceremonies Related to the Body Condition of the Brooder?

The linear regression with the highest adjusted R^2 value for the dependent measure, average total time, had mass and BUTY as the predictor variables. Both variables were significant, such that longer total sequence times were associated with lower body mass (Table 3; Figure 4A) and higher BUTY levels (Figure 4B). All other candidate models that included physiological and behavioral predictors had lower adjusted R^2 values (Table 3). The same pattern of results was obtained when the adjusted mass was used instead of the mass of the birds that were actually captured.

In contrast to the results for behavioral variables averaged across the chick-rearing period, there was no relationship between mass or BUTY and total time in the nest relief sequence closest to the time the bird was captured. In the model with the highest adjusted R^2, the significant predictor of the total sequence time when the focal bird was the brooder was the brooder's latency to allopreen in both the strongest models and the brooder's rate of allopreening in one of the models (Table 3). When the focal bird was the returner, the significant variables in the analyses with the highest adjusted R^2 values were the latency to allopreen by either partner and the difference in

latency to allopreen for the 2 birds (Table 3). Turn-taking ceremonies were longer when either partner started allopreening later and when the brooder took longer to reciprocate after the returner initiated allopreening.

In the matched-pairs analysis, low-quality brooders started to allopreen later (397.0 ± 67.8 s) than their high-quality mates did when they were brooders (211.7 ± 41.0 s, one-tailed $t = 1.99$, df = 7, $P = 0.043$). Low-quality brooders also departed later (840.3 + 110.3 s) than high-quality brooders (536.9 + 48.7 s, $t = 2.43$, df = 7, $P = 0.046$).

Finally, higher-quality birds (i.e. those with a higher proportion of visits in which they brought fish for the chick) had higher chick-feeding rates ($r = 0.67$, $P = 0.033$, $n = 11$) and, as brooders, shorter latencies to exchanging nest duties ($r = -0.46$, $P = 0.034$, $n = 21$).

DISCUSSION

Behavioral Interactions in Different Types of Turn-Taking Ceremonies

The 4 turn-taking ceremony types were successfully distinguished by total duration and by differences in allopreening rates, latencies, and symmetry (see Figure 2). Multiple Nest Relief sequences and No Fish sequences were longer than Regular Nest Relief and No Nest Relief sequences, but the latter 2 sequence types did not differ from each other in total time. Allopreening was asymmetrical in No Fish and No Nest Relief sequences, due to brooders starting to allopreen significantly later than returners. By contrast, allopreening was symmetrical in Regular Nest Relief and Multiple Nest Relief sequences but the onset typically occurred before the nest relief in the former and after the first nest relief in the latter (see Figure 2).

Total sequence time did not differ between Regular Nest Relief and No Nest Relief sequences (in which the returner departs), but the latency to allopreen by the brooder was significantly longer when no nest relief occurred. The delay in brooder allopreening in No Nest Relief ceremonies, plus the lack of difference in total time, suggests that Common Murres may refrain from allopreening to delay or prevent a nest relief. Similarly, when returners in No Fish sequences allopreen at a higher rate than in other sequence types, they may be attempting to hasten or facilitate a nest exchange. Despite this higher allopreening rate by the returner, No Fish nest reliefs were longer than most other types, possibly because the brooder in these sequences did not reciprocate for an extended period. Thus, it appears that once the returning mate lands at the nest site, the brooder controls whether and when the pair will exchange roles.

Allopreening has been suggested to function in pair-bond formation and maintenance, communication, and parasite removal, and as a reciprocal stress reducer (Kober and Gaston 2003, Lewis et al. 2007). Several researchers have
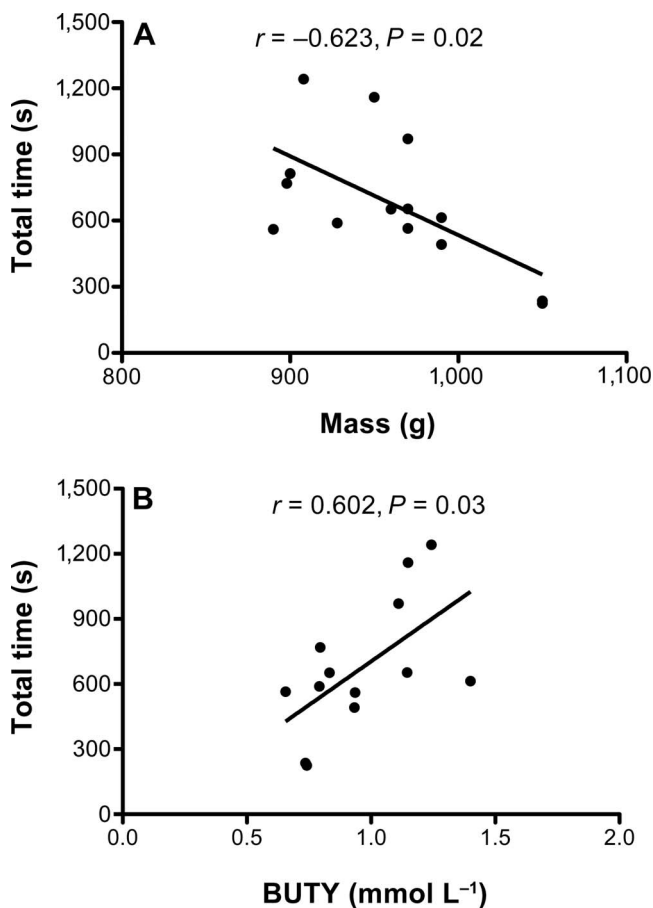
TABLE 3. Regression models for our study pairs of Common Murres, with total time of turn-taking ceremonies as the dependent measure and physiological and behavioral variables as predictors. Abbreviations: BUTY = beta-hydroxybutyrate, APL = allopreening latency, APR = allopreening rate, r = returner, b = brooder, and d = difference between value of returner and brooder. Significant predictors are in bold.

Predictor variables tested	F (P)	Adjusted R^2	Predictors (t, P, β)
Average of sequences across chick rearing			
Mass, BUTY	8.4 (0.01)	0.55	**Mass (−2.7, 0.03, −0.53); BUTY (2.6, 0.03, 0.50)**
Mass, APLd	7.3 (0.01)	0.49	**Mass (−2.2, 0.05, −0.47)**; APLd (2.0, 0.07, 0.44)
Mass, APLr	7.0 (0.01)	0.48	**Mass (−3.5, 0.01, −0.73)**; APLr (−1.9, 0.08, −0.40)
Closest sequence to capture—returner is focal bird			
APLr, APLb	11.24 (0.001)	0.51	**APLb (4.4, 0.001, 0.70); APLr (2.3, 0.03, 0.47)**
APLr, APLd	11.24 (0.001)	0.51	**APLd (4.4, 0.001, 0.92); APLr (4.2, 0.001, 0.88)**
Closest sequence to capture—brooder is focal bird			
APLb, APRb	8.75 (0.002)	0.44	**APLb (4.1, 0.01, 0.72); APRb (2.1, 0.05, 0.37)**
APLb, APLr	8.05 (0.003)	0.41	**APLb (3.6, 0.01, 0.61)**; APLr (−1.9, 0.08, −0.40)

noted that pair members with reciprocal allopreening bouts have more compatible relationships (e.g., Gill 2012), but Lewis et al. (2007) noted that while neighboring Common Murres have symmetrical allopreening bouts with each other, Common Murre mates do not. Our results suggest an additional function of allopreening: to negotiate parental duties. We suggest that allopreening patterns were symmetrical when neither bird (Regular Nest Relief) or both birds (Multiple Nest Relief) negotiated. When asymmetries occur, they appear to be used to negotiate which partner will start or continue brooding. Few previous studies have investigated the behavioral components of nest-duty negotiation (but see Boucaud et al. 2016).

Multiple Nest Reliefs in which the brooder eventually left had more bill-fencing bouts than those in which the returner departed, and it may be the case that a high level of persistence or aggression on the part of the returner is necessary to force an apparently reluctant brooder to depart. Bill fencing may reflect an escalation in the intensity of interactions that occur when allopreening interactions have not produced a smooth transition in brooding duty.

Relationship of Behavioral Variation to Body Condition

Average total sequence time was longer when brooding Common Murres weighed less and had higher BUTY levels. Higher BUTY levels mean that birds with longer turn-taking sequences were losing body mass at a higher rate than other individuals, even though adult mass is generally stable by the middle of the chick-rearing period. This stability in mass after the initial decrease may be the reason that mass was related to average behavioral rates but not to behavioral data from the single ceremony closest to capture. These findings suggest that when brooders withhold allopreening and postpone departure, they provide their mates with information about their poor body condition, supporting our contention that brooding is the less energetically costly parental activity. These results are consistent with the similar disruptions in turn-taking reported for Common Murres with data loggers (Wanless et al. 1988, Hamel et al. 2004).

FIGURE 4. Relationship of total time to (**A**) mass and (**B**) β-hydroxybutyrate (BUTY) levels in nest relief sequences in our study pairs of Common Murres in which the returner brought a fish.

Evidence of Negotiation

When returning Common Murres do not bring a fish or when brooders delay allopreening and nest exchanges, they may be communicating their condition to their mates and attempting to negotiate more brooding time. As Jones et al. (2002) argued, if a high level of care by both parents and mate retention are both necessary for successful reproduction, partners should compensate, if possible, when their partners negotiate to do less work. This compensation would help prevent the mate's condition from deteriorating to the abandonment threshold (Jones et al. 2002). In order to compensate when necessary, mates should be sensitive to any behavioral cues from their partners that indicate that the partner may be approaching that threshold. As several authors have pointed out, the extent of compensation may depend on the quality of information passing between the mates (Hinde 2006, Johnstone and Hinde 2006, Hinde and Kilner 2007). Thus, returners may be compensating for their mates when they go off to forage again after their mates do not give them access to brood the chick. Similarly, when returners arrive without a fish, their brooding mates may compensate for them by allowing a nest relief, even though the returners have not fulfilled the chick-provisioning component of turn-taking. These results are consistent with the Common Murre logger studies in which total feeding rates were not lower in pairs with one logger bird compared to controls (Wanless et al. 1998, Hamel et al. 2004), indicating that mates were compensating for the reduced provisioning rate of their logger-equipped partners.

This evidence of ongoing negotiation in chick-rearing Common Murres differs from research in some passerine systems where the results from handicap studies conform more closely to the "sealed bid" model of parental coordination (e.g., Schwagmeyer et al. 2002). Schwagmeyer et al. (2002) suggested that individual contributions in House Sparrows (*Passer domesticus*) may appear to be "sealed" because the actual negotiations took place earlier in incubation, when partners relieve each other directly and, therefore, know each other's contributions. That the negotiation apparently extends into chick rearing in Common Murres may reflect the fact that partners are still directly relieving each other, since one parent always broods the chick. Alternatively, this apparent extension of negotiation into chick rearing may reflect the greater daily variation in food availability for seabirds compared to passerines and, hence, greater variation in parental condition and need to continue negotiating.

Common Murres spend more time together during nest reliefs when foraging conditions are good than when they are poor (Cairns et al. 1987, Burger and Piatt 1990, Monaghan et al. 1994, Uttley et al. 1994, Zador and Piatt 1999, Wilhelm et al. 2008). Foraging conditions in the year of our study (2009) were unusually poor as a result of late inshore spawning of capelin (*Mallotus villosus*), the main fish species that Common Murres in this area feed their chicks (Regular et al. 2014). An interesting extension to this research would be to examine how negotiation and compensation during turn-taking are related to body condition under a wider range of foraging conditions and brooding-shift durations.

In summary, we consider that the following results may reflect parental negotiation: (1) long ceremonies were linked to poor body condition and the delayed onset of allopreening; (2) brooders appeared to delay or prevent nest reliefs by not reciprocating their mate's allopreening; and (3) returners arrived without a fish and initiated allopreening at a higher rate than birds that returned with a fish. While No Fish and No Nest Relief sequences may reflect only one of the partners negotiating (returner and brooders, respectively), Multiple Nest Reliefs may occur when both partners are negotiating for additional brooding time. Common Murres apparently compensate for their partners by allowing them to start or continue brooding without fulfilling the chick-provisioning component of turn-taking. Higher frequencies of bill fencing may signal that negotiations are not accepted. Our study may be one of the first to suggest that parental interactions at the nest involve pair members communicating their physiological status by negotiating behavioral duties in their own and their mate's mutual interest.

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