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Consistent individual variations in aggressiveness and a behavioral syndrome across breeding contexts in different environments in the Black-tailed Gull

Kentaro Kazama · Yasuaki Niizuma · Yutaka Watanuki

Abstract Individual behaviors of animals do not evolve separately; they do so in association with other behaviors caused by single shared genetic or physiological constraints and/or favored by selection. Thus, measuring behavioral syndromes—suites of correlated behaviors across different contexts—leads to a better understanding of the adaptive significance of variations in behaviors. However, relatively few studies have examined behavioral syndromes in wild animal populations in changing environments. We investigated a potential behavioral syndrome across antipredator nest defense, territorial defense, chick provisioning, and mating behaviors of male Black-tailed Gulls *Larus crassirostris* in two successive years under different conspecific territorial intrusion risks and food conditions. Males that presented high levels of antipredator nest defense (aggressive antipredator defenders) against a crow decoy (crows are egg predators) defended their territories against conspecific intruders more frequently than did other males (nonaggressive antipredator defenders), independent of the risk of intrusion. Aggressive antipredator defenders also fed their chicks more frequently than nonaggressive males, but only in a year of low food availability. Taken together, this indicates that males show consistent aggressiveness regardless of breeding context (antipredator and territorial defense), but can regulate food provisioning according to food availability.

Keywords Behavioral syndrome · Aggressiveness · Animal personality · Extra-pair copulation · Parental care

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Introduction

Among animals, individual behaviors generally do not evolve in isolation; they do so in association with multiple behaviors, because correlated multiple behaviors are constrained by a single genetic or physiological mechanism (Price and Langen 1992) and/or favored by selection (Bell 2005; Wolf et al. 2007). Consequently, animals often exhibit consistent inter-individual behavioral variation in multiple behavioral contexts, such as mating and foraging, without adaptive behavioral plasticity (i.e., environment-induced and/or context-dependent phenotypic change) (Wilson 1998; Gosling 2001). These consistent individual variations in suites of correlated behavioral traits are called behavioral syndromes (Sih et al. 2004). Measuring the breadth of a behavioral syndrome (which behaviors are correlated and which behaviors are not) enhances our knowledge of the processes of evolution and the adaptive significance of variations in such behaviors (Duckworth 2006).

The relationships among several aggressive contexts that often affect individual fitness—such as defense of a resource, competition for a mate, and antipredator behavior—are relatively well understood in some animal species (e.g., Riechert and Hedrick 1993; Sih et al. 2003; Duckworth 2006). Such a behavioral syndrome could also extend to several other nonaggressive contexts (e.g., foraging, exploration activity in a novel environment) (Sinn

et al. 2010; Wilson et al. 2010). Among birds, individuals exhibiting higher levels of aggression toward conspecific competitors also tend to exhibit higher levels of both antipredator aggression (Hollander et al. 2008) and activities relating to mating behavior (Day et al. 2006; van Oers et al. 2008), but lower levels of parental care (Ketterson et al. 1992; Magrath and Elgar 1997).

Recently, a few authors have demonstrated that environmental and social conditions may affect behavioral syndromes (e.g., Sinn et al. 2010). In wild populations of Dumpling Squid *Euprymna tasmanic*, for example, a behavioral syndrome for the relationship between responsiveness to predators (large fishes) and responsiveness to prey (shrimp) varies with environmental/social conditions, such as population density and adult sex ratio (Sinn et al. 2010). Understanding the relationship between environmental/social conditions and this behavioral syndrome provides insight into the constraints on behavioral evolution (Bell 2007; Bell and Sih 2007; Réale et al. 2007; Sinn et al. 2010). Thus, more studies that examine behavioral syndromes in changing environments are necessary. However, there have been many previous studies of behavioral syndromes that occur in captive reared animals in a consistent environment (Verbeek et al. 1994; Bell 2005). Indeed, behavioral syndromes have been identified in several wild animal species (Duckworth 2006; Bell and Sih 2007; Dingemanse et al. 2010), but the extent to which these behavioral syndromes change with the environment is relatively unexplored (but see Sinn et al. 2010).

In Black-tailed Gulls *Larus crassirostris*, there is considerable individual variation in male aggressiveness towards avian egg-predators, such as Jungle Crows *Corvus macrorhynchos*, but not in females (Kazama and Watanuki 2010). The antipredator aggressiveness of individual males highly consistently occurs specifically within the incubation period (approximately 30 days) and across years (Kazama and Watanuki 2010; Kazama et al. 2011). These consistent individual variations in antipredator aggressiveness are independent of body size, clutch size, the timing of egg-laying, and the age of the clutch, indicating that individual aggressiveness is not regulated plastically by those ecological factors (Kazama et al. 2010, 2011). In this species, males copulate with their mates and sometimes with other females, and defend more aggressively against conspecific territorial intruders than females, while males and females share chick food provisioning equally (Kazama 2010).

In this study, we examined four aspects of aggressiveness in relation to consistency and its relation to other behavioral characters. First, we examined the within- and between-year consistency (repeatability) of the antipredator aggression behaviors of individual males. We then measured the breadth of the behavioral syndrome for aggression and parental care in changing environments. We predicted that males exhibiting high levels of antipredator aggressiveness would also defend against conspecific intruders more vigorously, but care less for their offspring (i.e., perform less food provisioning for their chicks). At the same time, we examined whether the behavioral syndrome differed between years that had different risks of conspecific territorial intrusion and chick growth rates (a proxy for food condition). Finally, we examined the behavioral syndrome in the mating context in a single year. We predicted that males exhibiting high levels of antipredator aggressiveness would copulate with their mates and other females more frequently.

Methods

Study area and period

The study was conducted on Rishiri Island (45°14′N, 141°09′E), situated in the Sea of Japan 40 km off northern Hokkaido, Japan, from 25 April to 10 July in both 2007 and 2008. The island supported more than 19,000 breeding pairs of Black-tailed Gulls in 2004 (Kosugi et al. 2005). A study site (0.030 ha) in a subcolony was established at Oiso, on the gentle northwestern slope, and was used in 2007 (157 nests) and 2008 (107 nests). Nest contents were checked every one or two days. All of the nests in the study site were mapped and marked with numbered stakes immediately after the eggs were laid.

Identification of the study individuals

In 2007, the behaviors of 26 pairs of arbitrarily chosen nests were observed. To identify the sex of each gull, we observed male courtship feeding and copulation behavior before egg-laying with their primary mate. Further, to facilitate individual identification, black hair-dye (Bigen hair color, containing aminophenol and stearic acid as major ingredients; Hoyu Co., Ltd., Nagoya, Japan) was used during the incubation period: dyed stones or leaves were placed in the nest cups so that the dye would mark the breast or neck of either the male or female parent (whichever returned to incubate the eggs first). All males of these 26 pairs were captured by box or line trap in 2007 during the incubation period, and were banded with numbered plastic and metal rings. In 2008, 23 of these 26 males returned to the study site, and 20 bred. In addition to those 20 males, members of another 11 breeding pairs in the study site were marked with the dye and their behaviors were observed in 2008.

Between-year differences in the risk of territorial intrusion and food condition

Conspecific individuals (either nonbreeders or failed breeders) intrude upon breeding territories and attack and sometimes kill chicks during the chick-rearing period (Kazama 2010). We recorded the frequency of intrusions by conspecifics (the number of approaches to 0.5 m from the chicks) and the number of chicks killed by conspecific intruders while observing all of the nests in the study site.

To examine food conditions during the chick-rearing period, 18 and 12 chicks from two-chick broods in 2007 and 2008, respectively, were weighed to the nearest 1 g using a spring balance (Pesola AG, Baar, Switzerland) every five days. Since the chicks of most *Laridae* species, including the study species, increase in body mass linearly during the period from hatching to the date just before fledging (approximately 35 days old; Hunt and Hunt 1976; Watanuki 1992), the chick growth rate was calculated as the mean increase in mass (g/5 days) during the period for each chick. Chicks outside of the study site were used to do this, in order to minimize any disturbance of the birds under observation. In a previous study of Black-tailed Gulls, the dominant prey items during the chick-rearing period were Japanese Sand Lance *Ammodytes personatus* and Japanese Anchovy *Engraulis japonica* (Kazama et al. 2008b), which have higher energy densities (anchovy: 6.3–6.7 kJ/g wet mass, sand lance: 5.5–6.7 kJ/g) than other prey (e.g., sebastes and greenlings: 4.8–5.0 kJ/g, squids: 3.4 kJ/g) (Watanuki 1987; Takahashi et al. 2001). For 25 and 18 arbitrarily selected pairs in 2007 and 2008, respectively (not the 26 and 31 pairs at the study site mentioned above), we used the proportion of a feeding bout (i.e., "feeding session;" see below), measured by observation, that provided these dominant prey species as an index of food condition.

Antipredator aggression assay

We recorded the antipredator aggressiveness of 26 and 31 study individuals in 2007 and 2008, respectively, as responses to a model predator—a crow decoy (a plastic hunting decoy painted to resemble an American Crow *C. brachyrhynchos*; Carry-Lite Inc., Fort Smith, AR, USA) during the incubation period, following Kazama et al. (2011). The decoy was placed on the ground, 1.5 m distant from the nearest nest, and covered with a cloth. After 30 min (when the gulls had settled down), the decoy was exposed for 2 min by pulling on a line attached to the cloth.

During the presentation, most of the gulls within a 2.5 m radius of the decoy stopped incubating, stood up, and gave alert calls; several of them attacked the decoy, striking it with their bodies or legs. These responses of individual gulls to the crow decoy were similar to those directed at live Jungle Crows (Kazama and Watanuki 2010). During natural egg predation attempts by Jungle Crows, the first gulls to attack the crow successfully drove it away (within several seconds), and these first attackers were defined as the "first defenders" (Kazama and Watanuki 2010). The antipredator aggressiveness (first defender or not) was determined in a single instance for eight males, in two instances for 17 males, and in three instances for a single male in 2007. In 2008, aggressiveness was determined in one instance for 16 males, in two instances for four males, in three instances for eight males, and in four instances for three males. For 20 banded and returning males, antipredator aggressiveness was determined in both 2007 and in 2008.

Territorial and feeding behaviors

Territorial attendance, territorial defense, and feeding behaviors were observed during the daytime [0400–2000 hours Japan Standard Time (JST)] 3–4 days per week for 26 males from 3 June to 13 July 2007, and for 31 males from 30 May to 10 July 2008, yielding total observation times of 4,628 nest-hours in 2007 (mean 7.7 h/observation for 23 observations in total) and 7,650 in 2008 (10.2 h/ observation for 22 observations). In the Black-tailed Gull, pair-members alternate their stays at their territory and guard chicks (Narita and Narita 2004). Territorial attendance (<1 m from the radius of the nest cup) was recorded every 20 min. To maintain their breeding territories and to defend chicks, parents threaten (by opening their bills and wings) or attack (involving body contact) conspecific intruders (Kazama 2010). Parents are usually successful at driving intruders away with a single threat or attack. Some males, especially aggressive antipredator defenders, vigorously defended against gulls landing or walking several meters from the nest of the males, even if the gulls did not attack the chicks (approaches to within 0.5 m of the chicks) (K. Kazama, personal observation). Therefore, we used the number of incidents of territorial defense (threatening or attacking) and not the number of attacks per chick as our index of aggressiveness against conspecifics (see the "Statistical analysis" section below).

A "foraging trip" was defined as an occasion on which a parent left its nest for more than 30 min. When parents left for shorter periods (<30 min), they bathed and/or defecated and did not bring back food. Parents that had returned from a foraging trip fed their chicks several times intermittently while remaining in their territory. A "feeding session" was defined, therefore, as a single occasion when a parent provided food to one or more chicks.

Mating behavior in 2008

As we did not mark birds prior to the incubation period in 2007, mating and courtship behavior was not recorded in that year. The behaviors of 20 males that were banded in 2007 and returned and bred in 2008 were observed from 28 April to 7 May 2008, prior to egg-laying. From 0600 to 1000 hours (JST), we recorded attendance at the territory (<1 m from the radius of the nest cup) and the number of copulation attempts with their mates and with other females (extra-pair copulation; EPC). The total observation time was 338 male-hours during this period.

Statistical analysis

Between-year differences in the frequency of conspecific intrusion for each nest were examined using a linear mixed model (LMM), including the frequency as a dependent variable and year as a fixed effect. As 20 banded males were observed repeatedly in 2007 and 2008, male identity was included as a random effect in the models to avoid pseudo-replication. Each female and nonbanded male was regarded as another individual in the analyses for each year, even if they returned to the same nest sites across years. The proportion of chicks killed by conspecific intruders during the observations was compared between years using Fisher's exact test. The proportion of the feeding sessions that provided the dominant fish prey species (sand lance and anchovy) was compared between years, using a general linear model (GLM), with the proportion for each bird used as a dependent variable and year as an independent variable. Chick growth rates were compared between the years using one-way ANOVA.

To examine individual consistency of antipredator aggressiveness, within- and between-year repeatabilities (r) were estimated. Repeatability is given by $r = S_A^2/(S^2 + S_A^2)$, where S_A^2 is the variance among individuals and S^2 is the variance within individuals over time, and was calculated for binomial data to give the standard error and statistical significance following Nakagawa and Schielzeth ([2010]). Within-year repeatability was calculated for gulls where nest defense intensity (first defender or not) was measured more than twice within a year. Males that were the first defenders at least once in each year were scored as "aggressive antipredator defenders (score 1)" and the others were called "nonaggressive antipredator defenders (score 0)." Between-year repeatability was calculated as whether the male was a consistently aggressive or nonaggressive antipredator defender across years.

The data for territorial attendance, territorial defense, and feeding behaviors collected when the chicks were 10–25 days old were used in the analyses, since these activities peak during this chick age period in gulls (Pugesek [1983], [1990]). To examine the effects of behavioral trait (aggressive or non-aggressive antipredator defenders), year, and the interaction of those on territorial and feeding behaviors, we employed a generalized linear mixed model (GLMM) that included those frequencies or durations as dependent variables, and behavioral trait, year, and their interaction as fixed effects. Territorial attendance, recorded as whether the male attended their territory (1) or not (0) during each 20 min of observation time ($N = 4,870$), was assigned a binomial distribution with a logit link function, and territorial defense, recorded as the frequency of territorial attendance during each 20 min of observation time ($N = 2,192$) was assigned a Poisson distribution with a log link function. Foraging trip duration (minutes, $N = 206$) was assigned a gamma distribution with a log link function. Feeding session, recorded as whether the male fed his chicks (1) or not (0) during each arrival at the nest after foraging ($N = 373$), was assigned a binomial distribution with logit link function. Male identity was included as a random effect in those GLMMs to avoid pseudoreplication.

The frequency of copulation varied with the progress of breeding (Helfenstein et al. [2003]; Kempenaers et al. [2007]), so we used mating data from 1–6 days before egg-laying. To examine the differences in mating behavior between aggressive and nonaggressive antipredator defenders, we employed a GLMM that included those frequencies as dependent variables and behavioral trait (aggressive or nonaggressive antipredator defenders) as a fixed effect. Both copulation attempts with a mate, recorded as the frequency of copulation attempts with the mate when attending the territory during each 20 min ($N = 200$) and copulation attempts with a nonmate (EPC), recorded as the frequency of copulation attempts with a nonmate during each 20 min of observation time ($N = 331$), were assigned a Poisson distribution with a log link function. Male identity was included as a random effect in these GLMMs to avoid pseudoreplication.

For each GLMM, the p value for the significance of the effect of each factor was obtained from a likelihood ratio test comparing the likelihood of the model including the factor with that of the model not including the factor. All analyses in this study were performed using the lme4 package (Bates and Maechler [2010]) for R, v.2.12.1 (R Development Core Team [2010]).

Results

Between-year differences in the risks of intrusion and food condition

The frequency of territorial intrusion (mean ± SD) was greater in 2008 (0.45 ± 0.10 intrusions/h, $N = 107$ nests)

than in 2007 (0.10 ± 0.02, $N = 157$, LMM; $F_{1,262} = 8.50$, $p = 0.004$). The proportion of chicks killed by conspecific intruders during observation was greater in 2008 (19.2%, 34 of the 177 chicks hatched within the study site) than in 2007 (10.2%, 27 of 265, Fisher's exact test, $p = 0.01$).

The proportion of Japanese Sand Lance and Japanese Anchovy in the diet was greater in 2008 (0.795 ± 0.201, $N = 50$) than in 2007 (0.686 ± 0.258, $N = 36$, GLM; $F_{1,84} = 4.83$, $p = 0.03$). Chick growth rate also tended to be greater in 2008 (97.5 ± 13.8 g/5 days, $N = 12$) than in 2007 (89.1 ± 11.7 g/5 days, $N = 18$), though the difference was not statistically significant (one-way ANOVA; $F_{1,28} = 3.25$, $p = 0.08$).

These results indicated that the risk of conspecific territorial intrusion was higher in 2008 than in 2007, and that food conditions were worse in 2007 than in 2008.

Consistency of antipredator aggressiveness

Antipredator aggressiveness of males was highly repeatable within the year in both 2007 and 2008 (Table 1a), and also between years (Table 1b). Thirty-five percent of the males

(9/26 males) in 2007 and 39% (12/31) of them in 2008 were categorized as aggressive antipredator defenders; i.e., they were the first defenders at least once in each year.

Territorial behavior

Neither behavioral trait (aggressive or nonaggressive defender), year, nor the interaction of these factors affected territorial attendance (Table 2a; Fig. 1a). Both behavioral trait and year, but not the interaction of the two, affected the frequency of territorial defense (Table 2b). Frequency of territorial defense during each 20 min of territory attendance was higher for the aggressive antipredator defenders than the nonaggressive ones, and in 2008 than in 2007 (Fig. 1b).

Feeding behavior

Neither behavioral trait, year, nor the interaction of the two affected the duration of foraging trips, that is interval of returning to the nest from foraging (Tables 2a, 3). Either behavioral trait, year, or those interaction did affect the proportion of feeding session (Table 4). The proportion of

Table 1 Within-year repeatability (a) and between-year repeatability (b) of antipredator aggressiveness in male Black-tailed Gulls, and proportions of consistently antipredator aggressive or nonaggressive defenders, respectively

Year	Proportion of individuals displaying consistent defense behavior (%)[a,b]	Repeatability $(r) ± SE$	$N_{(2,3,4)}$	p
(a) Within-year repeatability				
2007	83.3	0.84 ± 0.24	17, 1, 0	<0.001
2008	93.3	0.99 ± 0.04	4, 8, 3	<0.001
(b) Between-year repeatability				
2007–2008	100	0.99 ± 0.02	20	<0.001

$N_{(2,3,4)}$ indicates numbers of individuals for which the intensity of nest defense was measured twice, three times, and four times in a year

[a] Proportion of individuals that were the first defender in every decoy presentation, or were never the first defender, within that year

[b] Proportion of individuals who were displayed antipredator aggression or who were nonaggressive defenders in both years

Table 2 The effects of behavioral trait (aggressive or nonaggressive defender), year, and the interaction of those two factors on (a) the proportion of territory attendance and (b) territorial defense for male Black-tailed Gulls (GLMM results)

Dependent variable	Fixed effect[a]	Parameter estimate	SE	χ^2	p
(a) Territorial attendance[b] ($N = 4,870$)	Behavioral trait	0.164	0.248	0.001	0.99
	Year	−0.133	0.158	0.67	0.41
	Behavioral trait × year	0.009	0.205	0.002	0.96
(b) Territorial defense[c] ($N = 2,192$)	Behavioral trait	0.600	0.282	8.03	<0.01
	Year	0.480	0.151	10.0	<0.01
	Behavioral trait × year	0.204	0.169	1.43	0.23

[a] Parameter estimates were calculated such that nonaggressive defenders and 2007 were assigned a value of 0, and aggressive defenders and 2008 were assigned a value of 1, respectively

[b] Whether the individual attended the breeding territory (1) or not (0) during each 20 min of observation time, and assigned a binomial distribution (logit link function)

[c] Frequency for each 20 min of territorial attendance, and assigned for Poisson distribution (log link function)

feeding session was higher for aggressive antipredator defenders than nonaggressive ones in 2007, but not in 2008 (Fig. 2b). Taken together, aggressive antipredator defenders fed their chicks more frequently than nonaggressive
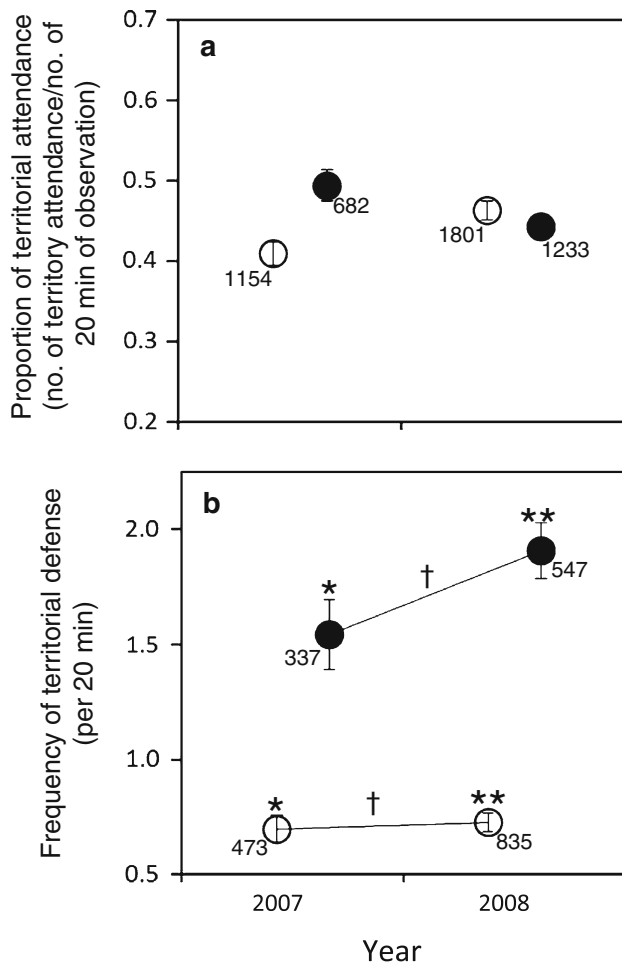

Fig. 1 Differences in the proportion of territorial attendance (a) and frequency of territorial defense (b) between nonaggressive (open circles) and aggressive antipredator defenders (filled circles) for male Black-tailed Gulls in 2007 and 2008. Error bar and number indicates the standard error and sample size, respectively. Asterisks and double asterisks indicates significant ($p < 0.01$) differences between aggressive and nonaggressive antipredators, and dagger symbols indicate significant ($p < 0.01$) differences between years

ones, but only during the year of lower food availability (in 2007).

Mating behavior in 2008

While aggressive antipredator defenders exhibited similar levels of copulation with their mates to nonaggressive defenders (Fig. 3a, GLMM: parameter estimates $\pm$ SE = 0.31 ± 0.32, $\chi^2 = 0.87$, $p = 0.35$), they attempted EPC more frequently than nonaggressive males (Fig. 3b, GLMM: parameter estimates $\pm$ SE = 1.46 ± 0.50, $\chi^2 = 6.82$, $p = 0.009$).

Discussion

Our study showed that antipredator aggressiveness was individually consistent both within- and between-years. Although our analyses were qualitative (dichotomic) rather than quantitative, this study also showed that antipredator aggressiveness was positively correlated with territorial aggressiveness regardless of the social condition (i.e., the risk of territorial intrusion). Antipredator aggressiveness was also correlated positively with feeding behavior, but only when food conditions were poor, and was positively correlated with EPCs. Therefore, we identified both environment-independent and -dependent behavioral syndromes in a single wild population.

Aggressive antipredator defenders that exhibited high levels of antipredator aggressiveness during the incubation period also defended their territories more frequently against conspecific territorial intruders during the chick-rearing period than did nonaggressive ones, in both 2007 and 2008. Such correlated aggression across two contexts has been observed in several animal species (Bell 2007). This behavioral syndrome across several aggression contexts may be related to instantaneous physiological effects. For example, in male Three-spined Sticklebacks Gasterosteus aculeatus, a correlation between individual aggressiveness in antipredator behavior and that in conspecific competition was considered to be a dual effect of gonadal steroid hormone (Huntingford 1976). Also in male Black-tailed Gulls,

Table 3 The effects of behavioral trait (aggressive or nonaggressive defender), year, and the interaction of those two factors on foraging trip duration for male Black-tailed Gulls (GLMM results)

Dependent variable	Fixed effect[a]	Parameter estimate	SE	χ^2	p
Foraging trip duration[b] ($N = 206$)	Behavioral trait	0.00004	0.00069	0.001	0.99
	Year	−0.00048	0.00055	0.001	0.99
	Behavioral trait × year	0.00072	0.00091	0.59	0.44

[a] Parameter estimates were calculated such that nonaggressive defenders and 2007 were assigned a value of 0, and aggressive defenders and 2008 were assigned a value of 1, respectively

[b] Assigned for gamma distribution (log link function)

aggressive antipredator defenders have higher levels of plasma testosterone during the early incubation period (Kazama et al. 2011).
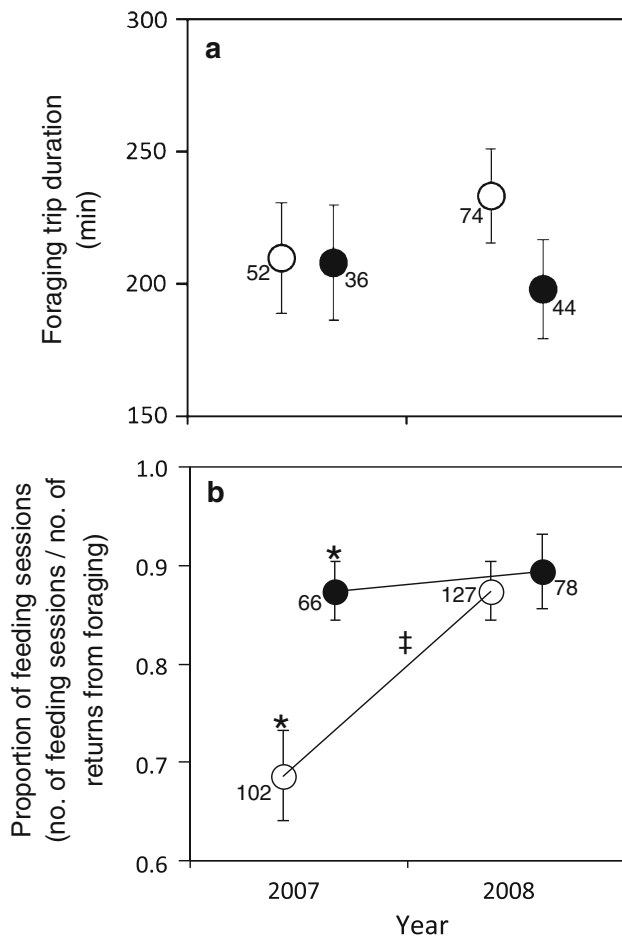

Fig. 2 Differences in foraging trip duration (**a**) and proportion of feeding sessions (the number of feeding sessions divided by the number of returns to the nest after foraging) (**b**) between nonaggressive (*open circles*) and aggressive antipredator defenders (*filled circles*) for male Black-tailed Gulls in 2007 and 2008. *Error bar* and *number* indicate the standard error and sample size, respectively. *Asterisks* indicates significant ($p < 0.01$) differences between aggressive and nonaggressive antipredators, and *dagger symbols* indicate significant ($p < 0.01$) differences between years. The interaction between behavioral trait and year (i.e., aggressiveness × year) was also significant ($p < 0.05$)

In Black-tailed Gulls, plasma testosterone levels decline rapidly after egg-laying (Kazama et al. 2008a), but individual aggressiveness was carried over from the incubation period to the chick-rearing period. This consistent aggressiveness across two contexts was maintained similarly in years with both high and low intrusion risks. These observations indicate that the individually consistent aggressiveness may be constrained by not only the instantaneous level of plasma testosterone but also certain long-term-consistent (lasting at least two years) physiological factors; for example, metabolic rate and some neurochemicals, as reviewed by Sih and Bell (2008). Further, recent work focusing on a natural population of Australian Lizards *Egerina whitii* has demonstrated individual consistency in the baseline level of testosterone (i.e., after the seasonal peak in its level) and that this is linked with consistent individual aggression (While et al. 2010).

Among several animal species, including birds, males that exhibit high levels of aggressiveness suppress parental investment (e.g., less feeding of offspring), since they spend more time and energy on aggressive interactions, attracting mates, or seeking EPCs (Ketterson et al. 1992; Clark and Galef 1999; Stoehr and Hill 2000; Magrath and Komdeur 2003). However, aggressive antipredator defenders fed chicks more frequently than nonaggressive ones in 2007 (during which there were poorer food conditions), and similarly frequently in 2008 (when there were better food conditions; see Fig. 2a, b). In some birds that have multiple breeding and mating opportunities during their lifetimes, when the female uses the male's parental investment and behavior as an indicator of his quality as a mate and his future behavior as a parent, males with a high level of aggressiveness increase investment in their offspring ("the good-parent hypothesis," Schwagmeyer and Mock 2003; Pampoulie et al. 2004). Long-lived Black-tailed Gulls (which can live over 20 years, Narita and Narita 2004) can have many future breeding opportunities during their lifetimes. Thus, aggressive defenders may not suppress their investment in their chicks, in order to demonstrate their high levels of investment as parents to current mates and/or future mates (e.g., other females).

Table 4 The effects of individual behavioral trait (aggressive or nonaggressive defender), year, and the interaction of these two factors on the proportion of feeding sessions for male Black-tailed Gulls (GLMM results)

Dependent variable	Fixed effect[a]	Parameter estimate	SE	χ^2	p
Feeding session[b] ($N = 373$)	Behavioral trait	2.769	1.077	7.24	0.007
	Year	1.217	0.369	11.31	<0.001
	Behavioral trait × year	−1.319	0.669	4.00	0.045

[a] Parameter estimates were calculated such that nonaggressive defenders and 2007 were assigned a value of 0, and aggressive defenders and 2008 were assigned a value of 1, respectively

[b] Whether the male fed his chicks (1) or not (0) during each trip to the nest after foraging, assigned a binomial distribution (logit link function)
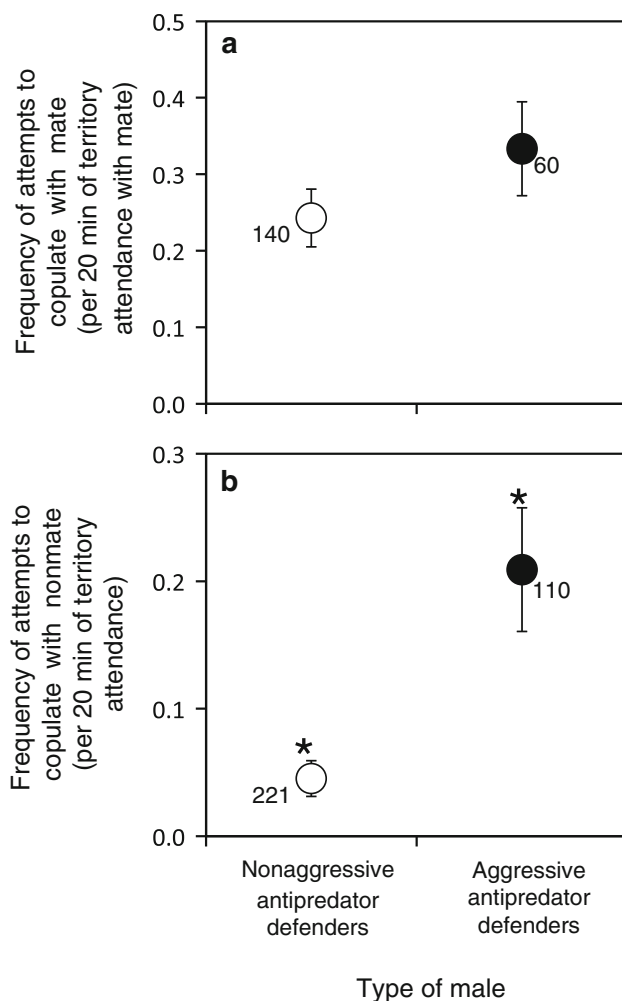
Fig. 3 Differences in the frequency of copulation attempts with mates (**a**) and nonmates (**b**) between nonaggressive (*open circles*) and aggressive antipredator defenders (*filled circles*) for male Black-tailed Gulls in 2008. *Error bar* indicates the standard error. *Asterisks* indicate significant ($p < 0.01$) differences between aggressive and nonaggressive antipredators

Aggressive antipredator defenders attempted copulations with extra-pair females more frequently than did nonaggressive ones. In Great Tits *Parus major*, bold and aggressive males (more explorative males) may intrude into the territories of other breeders and attempt EPCs more frequently and easily than shy and nonaggressive ones (van Oers et al. 2008). In Black-tailed Gulls, females that were mounted by extra-pair males showed intimidating actions (opening their bills and wings) to prevent the EPC (K. Kazama, personal observation). Aggressive antipredator defenders may have a greater ability to circumvent such defensive actions by females, allowing them to attempt EPC more easily than nonaggressive males.

Alternatively, aggressive antipredator defenders might be more attractive to females. In Great Tits, as the rate of extra-pair fertilization correlates with boldness (which is related to

aggressiveness), such consistent individual behavioral traits could affect mate attractiveness (van Oers et al. 2008). Also in Black-tailed Gulls, aggressive antipredator defenders that show higher levels of defensive behavior against predators and conspecifics might be more attractive to females, so they may perform more EPCs than nonaggressive defenders. However, no relationship between individual aggressiveness and extra-pair fertilization was found for Western Bluebirds *Sialia mexicana* (Duckworth 2006). The motivation of females to perform EPCs and the actual fitness benefit for males of such EPCs (i.e., extra-pair fertilization) were completely unclear in this study.

Although theoretical research suggests that environmental and social conditions can influence the emergence of a behavioral syndrome (Rands et al. 2003; Dall et al. 2004), there have been a few empirical studies on this topic (reviewed by Dingemanse et al. 2010; but see Sinn et al. 2010). Our study empirically demonstrated that an environmental condition (i.e., food availability), but not a social condition (i.e., intrusion risk), affected the form of the behavioral syndrome in a single wild population. While aggressive antipredator defenders maintained their higher feeding rate despite changes in food conditions, nonaggressive males regulated their feeding rate according to such changes (Fig. 2b). Thus, the correlation between antipredator nest defense and feeding behavior (i.e., differences in feeding rate between aggressive and nonaggressive defenders) disappeared in 2008 (Fig. 2b). This indicates that individual behavioral plasticity (environmentally induced phenotypic change) in the context of feeding can differ between aggressive and nonaggressive defenders. A link between a behavioral syndrome and behavioral plasticity has recently been observed in a few wild animal species, although the adaptive significance of such a linkage is still unclear (Dingemanse et al. 2010). Longer-term observations and further studies of the fitness consequences both of aggressive and nonaggressive antipredator behavior in fluctuating environments are required to clarify the adaptive significance of and selection mechanism for the observed behavioral syndrome.

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