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Instructions for use

Consistent individual variation in aggressiveness and behavioral syndrome across

breeding contexts in changing environment in the Black-tailed Gull

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**ABSTRACT**

Individual behaviors of animals do not evolve separately but do so in association with other behaviors caused by single shared genetic or physiological constraints and/or favored by selection. Measuring behavioral syndrome which are suites of correlated behaviors across different contexts, therefore, provides better understanding of the adaptive significance of variations in behaviors. However, studies that have examined the behavioral syndrome in wild animal populations in changing environments are in the minority. We measured behavioral syndrome among anti-predator nest defense, territorial defense, chick-provisioning, and mating behavior of male Black-tailed Gulls *Larus crassirostris* in two successive years with different conspecific territorial intrusion risks and food conditions. Males with high levels of anti-predator nest defense (aggressive anti-predator defenders) against the decoy of crows (an egg-predator) defended their territory against conspecific intruders more frequently than did other males (non-aggressive anti-predator defenders) independently of the risk of intrusion. Aggressive anti-predator defenders also fed their chicks more frequently than non-aggressive males, but only in the year of lower food availability. Taken together, this indicates that males show consistent aggressiveness regardless of breeding context (anti-predator and territorial defense), but they can regulate food provisioning according to food availability.


Key words: behavioral syndrome, aggressiveness, animal personality, extra-pair copulation, parental care

# INTRODUCTION

Among animals, a single behaviors generally do not evolve in isolation, but 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 the suites of correlated behavioral traits are called behavioral syndromes (Sih et al. 2004). Measuring the breadth of behavioral syndrome (which behaviors correlate and which behaviors not) provides knowledge relevant to the processes of evolution and adaptive significance of variations in the behaviors (Duckworth 2006).

The relationships among several aggressive contexts, which would often affect individual fitness, such as defense of a resource, competition for a mate, and anti-predator behavior are relatively well-understood in some animal species (e.g. Riechert and Hedrick 1993; Sih et al. 2003; Duckworth 2006). Such behavioral syndrome could also extend to several other non-aggressive contexts (e.g. foraging, exploration activity in novel environment) (Sinn et al. 2010; Wilson et al. 2010). Among birds, individuals exhibiting higher levels of aggression toward conspecific competitors tend to also exhibit higher levels of both anti-predator aggression (Hollander et al. 2008) and activity in mating behavior (Day et al. 2006; van Oers et al. 2008), but lower levels of parental care (Ketterson et al. 1992; Magrath and Elger 1997).

Recently a few authors have demonstrated that environmental and social

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conditions may affect behavioral syndrome (e.g. Sinn et al. 2010). In wild populations of Dumpling Squid *Euprymna tasmanic*, for example, behavioral syndrome measured as the relationships between responsiveness to the predator (large fishes) and those to prey species (shrimp) varies with the environmental/social conditions such as population density and adult sex ratio (Sinn et al. 2010). Understanding the relationships between environmental/social conditions and this behavioral syndrome provides insight into the constraints of the evolution of behaviors (Bell 2007; Bell and Sih 2007; Réale et al. 2007; Sinn et al. 2010). Thus, more studies aimed examining behavioral syndromes in changing environments are necessary. Many previous studies of behavioral syndromes, however, have been documented in captive reared animals under consistent environment (Verbeek et al. 1994; Bell 2005). To date, behavioral syndrome 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 environments is relatively unexplored (but see Sinn et al. 2010).

In male Black-tailed Gulls *Larus crassirostris*, there is considerable individual variation in aggressiveness against avian egg-predators, such as Jungle Crows *Corvus macrorhynchos*, but not in females (Kazama and Watanuki 2010). The anti-predator aggressiveness of individual males is highly consistent within the incubation period (approximately 30 days) and across years (Kazama and Watanuki 2010, Kazama et al. 2011). These consistent individual variations in anti-predator aggressiveness are independent either of the body size, clutch size, timing of egg-laying, or age of the clutch, indicating that the individual aggressiveness was not regulated plastically with those ecological factors (Kazama et al. 2010; Kazama et al. 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 within- and between-year consistency (repeatability) of anti-predator aggression behavior of individual males first. Then, we measured the breadth of behavioral syndrome in aggression and parental-care context in changing environments. We predicted that males exhibiting high levels of anti-predator aggressiveness would also defend against conspecific intruders more vigorously, but less care their offspring (i.e. less provision to the chicks). Simultaneously we examined whether the behavioral syndrome differed between years with different risk of conspecific territorial intrusion and chick growth rate (proxy of food condition). Finally, we examined the behavioral syndrome in mating context in single year. We predicted males exhibiting high levels of anti-predator aggressiveness would copulate with their mates and other females more frequently.

**METHOD**

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 (0.030ha) in a sub-colony 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 the nests in the study site were mapped and marked with numbered stakes immediately after eggs were laid.

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Identification of the study individuals

In 2007, behaviors of arbitrarily-chosen pairs of 26 nests were observed. To identify sex of the gulls, we observed males' 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, twenty-three 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 by the dye and their behavior was observed in 2008.

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

Conspecific individuals (either non-breeders 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 during observations for all the nests in the study site.

To examine food conditions during the chick-rearing period, 18 and 12 chicks of 2-chick broods in 2007 and 2008, respectively, were weighed to the nearest 1 g using a spring balance (Pesola AG, Baar, Switzerland) every 5 days. Since the chicks of most

*Laridae* species including study species increase their body mass linearly during the period from hatching to date just before fledging (approximately 35-days old; Hunt and Hunt 1976, Watanuki 1992), the chick growth rate was calculated as the mean increment of mass (g/5days) during the period for each chick. For this purpose, chicks out of the study site were used to reduce disturbance of 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 had higher energy density (Anchovy: 6.3-6.7 kJ/g wet mass, Sand Lance: 5.5-6.7 kJ/g) than other non-dominant preys (e.g. Sebastes and Greenlings: 4.8-5.0 kJ/g, Squids: 3.4 kJ/g) (Watanuki 1987; Takahashi et al. 2001). So as an index of food condition, for an arbitrarily-selected 25 and 18 pairs in 2007 and 2008 respectively (different pairs from 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.

Anti-predator aggression assay

The anti-predator aggressiveness of 26 and 31 study individuals in 2007 and 2008, respectively, was recorded as responses to a model predator, i.e. a crow decoy (a plastic hunting decoy painted to resemble an American Crow *C. brachyrhynchos*; Carry-Lite Inc., Fort Smith, Arkansas) 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 minutes (when the gulls had settled down), the decoy was exposed for two minutes 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 made to live Jungle Crows (Kazama and Watanuki 2010). During natural egg predation attempts by Jungle Crows, the first gulls to attack the crow were successful in droving it away (within several seconds) and these first attackers were defined as "first defenders" (Kazama and Watanuki 2010). The anti-predator aggressiveness (first defender or not) was determined in a single instance in 8 males, 17 males in two instances, and in a single male in three instances in 2007. In 2008, aggressiveness was determined in 16 males in one instance, in 4 males in two instances, in 8 males in three instances, and in 3 males in four instances. For 20 banded and returning males, anti-predator aggressiveness was determined both in 2007 and in 2008.

Territorial and feeding behaviors

Territorial attendance, territorial defense, and feeding behaviors were observed during the daytime (04:00 - 20:00 h Japan Standard Time [JST]) for 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, giving observation times of 4,628 nest-hours in 2007 (mean 7.7 hours/observation for 23 observations in total) and 7,650 in 2008 (10.2 hours/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 minutes. To maintain their breeding territories and to defend chicks, parents threaten (by opening the bill and wings) or attack (involving body contact) conspecific intruders (Kazama 2010). Parents are usually successful in driving intruders away with a single threat or attack. Some males, especially aggressive

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anti-predator 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 attack per chick as our index of aggressiveness against conspecifics (see below statistical analyses section).

A "foraging trip" was defined as an occasion on which a parent left its nest for more than 30 minutes. When parents left for shorter periods (<30 minutes) 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 on the 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 06:00 to 10:00 h (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 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. All females and non-banded males were 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 observation was compared between years using Fisher's exact test. The proportion of the feeding sessions providing dominant fish prey species (sand lance and anchovy) was compared between years, using general linear model (GLM), with the proportion for each bird as a dependent variable and year as a independent variable. Chick growth rates were compared between the years using one-way ANOVA.

To examine individual consistency of anti-predator aggressiveness, within- and between-year repeatability ($r$) was 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 standard error and statistical significance following Nakagawa and Schielzeth (2010). Within-year repeatability was calculated for gulls where nest defense intensity (the 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 anti-predator defenders (score=1)" and the others were called "non-aggressive anti-predator defenders (score=0)". Between-year repeatability was calculated as whether the male was a consistently aggressive or non-aggressive anti-predator defender across years.

The data of territorial attendance, territorial defense, and feeding behaviors collected only when 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 effect of behavioral trait (aggressive or non-aggressive anti-predator defenders), year, and those interaction on territorial and feeding behaviors, we employed Generalized Linear Mixed Model (GLMM) including those frequencies or duration as dependent variables, and behavioral trait, year, and the interaction as fixed effects. Territorial attendance recorded as whether male attended at their territory (1) or not (0) for each 20 minutes of observation unit-time (N=4870) was assigned for binomial distribution with logit link function, and territorial defense recorded as the frequency for each 20 minutes of territorial attendance (N=2192) was assigned for Poisson distribution with log link function. Foraging trip duration (minutes, N=206) was assigned for gamma distribution with log link function. Feeding session recorded as whether male fed their chicks (1) or not (0) for each arriving to the nest from foraging (N=373) was assigned for binomial distribution with logit link function. Male identity was included as a random effect in those GLMMs to avoid pseudo-replication.

The frequency of copulation varied with the progress of breeding (Helfenstein et al. 2003; Kempenaers et al. 2007), therefore, we used mating data form 1-6 days before egg-laying. To examine the differences in mating behaviors between aggressive and non-aggressive anti-predator defenders, we employed GLMM including those frequencies as dependent variables and behavioral trait (aggressiveness or non-aggressive anti-predator defenders) as a fixed effect. Both copulation attempts with a mate recorded as the frequency for each 20 minutes of territorial attendance with mate (N=200), and copulation attempts with a non-mate (EPC) recorded as the frequency for each 20 minutes of observation unit-time (N=331), were assigned for Poisson distribution with log link function. Male identity was included as a random

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effect in these GLMMs to avoid pseudo-replication.

For each GLMM, significant p-value of each factor was obtained from likelihood ratio test comparing the likelihood of the model including the factor and that of the model not including the factor. All analyses of this study were performed using lme4 package (Bates and Maechler 2010) for R ver. 2.12.1 (R Development Core Team 2010).

## RESULTS

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

The frequency of territorial intrusion (mean $\pm$SD) was greater in 2008 (0.45 $\pm$0.10 intrusions/hr, N=107 nests) than 2007 (0.10 $\pm$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 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 $\pm$0.201, N=50) than in 2007 (0.686 $\pm$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 $\pm$13.8 g/5days, N=12) than 2007 (89.1 $\pm$11.7 g/5days, 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 food conditions were worse in 2007 than in 2008.

Consistency of anti-predator aggressiveness

Anti-predator aggressiveness of males was highly repeatable within a year in both 2007

and 2008 (Table 1a), and also between years (Table 1b). Thirty-five percent of males (9/26 males) in 2007 and 39% (12/31) in 2008 were categorized as aggressive anti-predator defenders, i.e. the first defenders at least once in each year.

Territorial behavior

Neither behavioral trait (aggressive or non-aggressive defenders), year, nor those interaction affected territorial attendance (Table 2a and Fig. 1a). Both behavioral trait and year, but not those interaction, affected the frequency of territorial defense (Table 2b). Frequency of territorial defense for each 20 minutes of territorial attendance was higher for aggressive anti-predator defenders than non-aggressive ones, and for in 2008 than in 2007 (Fig. 1b).

Feeding behavior

Neither behavioral trait, year, nor those interaction affected the duration of foraging trips, that is interval of returning to the nest from foraging (Table 3 and Fig. 2a). Either behavioral trait, year, or those interaction did affect the proportion of feeding session (Table 4). The proportion of feeding session was higher for aggressive anti-predator defenders than non-aggressive ones in 2007, but not in 2008 (Fig. 2b). Taken together, aggressive anti-predator defenders fed their chicks more frequently than non-aggressive ones only in the year of lower food availability (in 2007).

Mating behavior in 2008

While aggressive anti-predator defenders exhibit similar levels of copulation with their mates as non-aggressive defenders did (Fig. 3a, GLMM: Parameter

estimates±SE=0.31±0.32, $\chi^2$=0.87, p=0.35), they attempted EPC more frequently than non-aggressive males (Fig. 3b, GLMM: Parameter estimates±SE=1.46±0.50, $\chi^2$=6.82, p=0.009).

## DISCUSSION

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

Aggressive anti-predator defenders, exhibiting high levels of anti-predator aggressiveness during the incubation period, also defended their territories more frequently against conspecific territorial intruders during the chick-rearing period than did non-aggressive ones, both in 2007 and 2008. Such correlated aggression across two contexts was observed in several animal species (Bell 2007). The behavioral syndrome across several aggression contexts might be related with instantaneous physiological effects. For example, in male Three-spined Sticklebacks *Gasterosteus aculeatus,* a correlation between individual aggressiveness in anti-predator behavior and that in conspecific competition was considered to be the dual effect of gonadal steroid hormone (Huntingford 1976). Also in male Black-tailed Gulls, aggressive anti-predator defenders have higher levels of plasma testosterone during the early incubation period (Kazama et

al. 2011).

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

Among several animal species, including birds, males exhibiting high levels of aggressiveness suppress parental investment (e.g. less feeding for offspring) since they spend more time and energy for 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 anti-predator defenders fed chicks more frequently than non-aggressive ones in 2007 with poorer food conditions, and similarly frequently in 2008 with better food conditions (Fig. 2a and b). In some birds having multiple breeding and mating opportunity in the lifetime, when female use a male's parental investment and behavior as an indicator of his quality of mate and future behavior as parent, males representing high level of aggressiveness increase investment into offspring ("the good-parent" hypothesis, Schwagmeyer and Mock 2003, Pampoulie et al. 2004). Long-lived Black-tailed Gulls (over 20 years in maximum, Narita & Narita

2004) could have many future breeding opportunities in their lifetime. Thus, aggressive defenders might not suppress their investment into chicks to display their high investment as parent to current mate and/or future mate (e.g. other females).

Aggressive anti-predator defenders attempted copulations with extra-pair females more frequently than did non-aggressive ones. In Great Tits *Parus major*, bold and aggressive males (more explorative males), may intrude into the territory of other breeders and attempt EPCs more frequently and easily than shy and non-aggressive ones (van Oers et al. 2008). In Black-tailed Gulls, females that were mounted by extra-pair males showed intimidating actions (by: opening the bill and wings) to prevent the EPC (K. Kazama, personal observation). Aggressive anti-predator defenders may have higher ability to counterattack against females' defense and could be able to attempt extra-pair copulation more easily than non-aggressive males.

Alternatively, aggressive anti-predator defenders might be attractive for females. In Great Tits, as the rate of extra-pair fertilization can correlate with boldness in relation to aggressiveness, such consistent individual behavioral traits could affect mate attractiveness (van Oers et al. 2008). Also in Black-tailed Gulls aggressive anti-predator defenders that have higher level of defense against predators and conspecifics might be more attractive to females, and thus they could make EPCs relatively more frequently. However, no relationship between individual aggressiveness and extra-pair fertilization was shown in Western Bluebirds *Sialia mexicana* (Duckworth 2006). The motivation of females to EPCs and actual fitness benefit for males from the EPCs (i.e. extra-pair fertilization) were completely unclear in this study.

Although theoretical research suggests that environmental and social conditions could influence the emergence of behavioral syndrome (Rands et al. 2003,

Dall et al. 2004), there have been a few empirical studies (reviewed by Dingemanse et al. 2010, but see Sinn et al. 2010). Our study empirically demonstrated that environmental condition (i.e. food availability), but not social condition (i.e. intrusion risks), affected the shape of behavioral syndrome in a single wild population. While aggressive anti-predator defenders could maintain higher level of feeding rate despite of food condition change, non-aggressive males regulated their feeding rate to the change (Fig. 2b). Thus correlation between anti-predator nest defense and feeding behavior (i.e. differences in feeding rate between aggressive and non-aggressive defenders) disappeared in 2008 (Fig.2b). These indicated that individual behavioral plasticity (environmental induced phenotypic change) in the context of feeding could differ between aggressive and non-aggressive defenders. Linkage between behavioral syndrome and behavioral plasticity is recently observed in a few wild animal species, though adaptive significance of the linkage is still unclear (Dingemanse et al. 2010). Longer-term observation and further studies of fitness consequences both of aggressive and non-aggressive anti-predator defenders under the fluctuating environments are required to clarify the adaptive significance and selection mechanism of the observed behavioral syndrome.

## REFERENCES

Bates D, Maechler M (2010). lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-37. http://CRAN.R-project.org/package=lme4

Bell AM (2005) Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). J Evol Biol 18:464-473.

Bell AM (2007) Future directions in behavioural syndromes research. Proc R Soc B-Biol Sci 274:755-761.

Bell AM, Sih A (2007) Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). Ecol Lett 10:828-834.

Clark MM, Galef BG (1999) A testosterone-mediated trade-off between parental and sexual effort in male mongolian gerbils (*Meriones unguiculatus*). J Comp Psychol 113:388-395.

Dall SRX, Houston AI, McNamara JM (2004) The behavioural ecology of personality: consistent individual differences from an adaptive perspective. Ecol Lett 7:734-739.

Day LB, McBroom JT, Schlinger BA (2006) Testosterone increases display behaviors but does not stimulate growth of adult plumage in male golden-collared

manakins (*Manacus vitellinus*). Horm Behav 49:223-232.

Dingemanse NJ, Kazem AJN, Reale D, Wright J (2010) Behavioural reaction norms: animal personality meets individual plasticity. Trends Ecol Evol 25:81-89.

Duckworth RA (2006) Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. Behav Ecol 17:1011-1019.

Gosling SD (2001) From mice to men: what can we learn aboutpersonality from animal research? Psychol Bull 127:45–86.

Helfenstein F, Wagner RH, Danchin E, Rossi JM (2003) Functions of courtship feeding in Black-legged Kittiwakes: natural and sexual selection. Anim Behav 65:1027-1033.

Hollander FA, Van Overveld T, Tokka I, Matthysen E (2008) Personality and nest defence in the great tit (*Parus major*). Ethology 114:405-412.

Hunt GLJ Hunt MW (1976) Gull chick survival: the significance of growth rates, timing of breeding and territory size. Ecol 57: 62–75.

Huntingford FA (1976) The relationship between anti-predator behavior and aggression among conspecifics in Three-spined Stickleback. Anim Behav 24:245-260.

Kazama K (2010) Individual differences in aggressiveness and the function in the breeding colony in Black-tailed Gulls. Ph.D. Thesis, Hokkaido-University, Hokkaido, Japan. (in Japanese)

Kazama K, Niizuma Y, Watanuki Y (2010) Experimental study of the effect of clutch size on nest defense intensity in Black-tailed Gulls. Ornith Sci 9:93-100.

Kazama K, Niizuma Y, Sakamoto QK, Watanuki Y (2011) Factors affecting individual variation in nest defense intensity in colonially breeding Black-tailed Gulls. Can J Zool 89:938-944.

Kazama K, Sakamoto QK, Watanuki Y (2008a) Plasma testosterone levels of incubating Black-tailed Gulls. J Yamashina Inst Ornithol 39:112-116. (in Japanese with English abstract)

Kazama K, Tomita N, Ito M, Niizuma Y, Takagi M, Watanuki Y (2008b) Responses in breeding behaviour of Black-tailed Gull *Larus crassirostris* to different marine environments. In: Okada H, Mawatari SF, Suzuki N, Gautam P (eds) Proceedings of International Symposium "The Origin and Evolution of Natural diversity", 1-5 October 2007, Sapporo. Hokkaido-University Press, Sapporo, pp. 215-220.

Kazama K, Watanuki Y (2010) Individual differences in nest defense in the colonial breeding Black-tailed Gulls. Behav Ecol Sociobiol 64:1239-1246.

Kempenaers B, Lanctot RB, Gill VA, Hatch SA, Valcu M (2007) Do females trade copulations for food? An experimental study on kittiwakes (*Rissa tridactyla*). Behav Ecol 18:345-353.

Ketterson ED, Nolan VJr, Wolf L, Ziegenfus C (1992) Testosterone and avian life histories: effects of experimentally elevated testosterone on behavior and correlates of fitness in Dark-eyed Junco *Junco hyemalis*. Am Nat 140:980-999.

Kosugi K, Sugimura N, Sato M (2005) Breeding colony status of Black-tailed Gull in Rishiri Island, northern Hokkaido (1) Estimated population from 2002–2004. Rishiri Kenkyu 24:29-35. (in Japanese with English abstract)

Magrath MJL, Elgar MA (1997) Parental care declines with increased opportunity for extra-pair matings in fairy martins. Proc R Soc B-Biol Sci 264:1731-1736.

Magrath MJL, Komdeur J (2003) Is male care compromised by additional mating opportunity? Trends Ecol Evol 18:424-430.

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Narita K, Narita A (2004) Observation Reports of Black-tailed Gull. Kimura-Syoten, Hachinohe. (in Japanese)

Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biol Rev 85:935-956.

van Oers K, Drent PJ, Dingemanse NJ, Kempenaers B (2008) Personality is associated with extrapair paternity in great tits, *Parus major*. Anim Behav 76:555-563.

Pampoulie C, Lindstrom K, St Mary CM (2004) Have your cake and eat it too: male sand gobies show more parental care in the presence of female partners. Behav Ecol 15:199-204.

Price T, Langen T (1992) Evolution of correlated characters. Trends Ecol Evol 7:307-310.

Pugesek BH (1983) The relationship between parental age and reproductive effort in the California Gull *Larus californicus*. Behav Ecol Sociobiol 13:161-171.

Pugesek BH (1990) Parental effort in the California Gull - tests of parent-offspring conflict theory. Behav Ecol Sociobiol 27:211-215.

R Developmental Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN3-900051-07-0, URL http://www.R-project.org

Rands SA, Cowlishaw G, Richard A, Pettifor RA, Marcus J, Rowcliffe JM, Johnstone RA (2003) Spontaneous emergence of leaders and followers in foraging pairs. Nature 423:432-434.

Riechert SE, Hedrick AV (1993) A test for correlations among fitness-linked behavioral traits in the Spider *Agelenopsis aperta*. Anim Behav 46:669-675.

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal

temperament within ecology and evolution. Biol Rev 82:291-318.

Schwagmeyer PL, Mock DW (2003) How consistently are good parents good parents? Repeatability of parental care in the House Sparrow *Passer domesticus*. Ethol 109:303-313.

Sih A, Bell AM (2008) Insights for behavioral ecology from behavioral syndromes. In: *Advances in the Study of Behavior, Vol.38.* Elsevier Academic press, San Diego. pp.227-281.

Sih A, Bell AM, Johnson JC Ziemba RE (2004) Behavioral syndromes: An integrative overview. Q Rev Biol 79:241-277.

Sih A, Kats LB, Maurer EF (2003) Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish-salamander system. Anim Behav 65:29-44.

Sinn DL, Moltschaniwskyj NA, Wapstra E, Dall SRX (2010) Are behavioral syndromes invariant? Spatiotemporal variation in shy/bold behavior in squid. Behav Ecol Sociobiol 64:693-702.

Stoehr AM, Hill GE (2000) Testosterone and the allocation of reproductive effort in male House Finches *Carpodacus mexicanus*. Behav Ecol Sociobiol 48:407-411.

Takahashi A, Kuroki M, Niizuma Y, Kato A, Saitoh S, Watanuki Y (2001) Importance of the Japanese anchovy (*Engraulis japonicus*) to breeding rhinoceros auklets, (*Cerorhinca monocerata*) on Teuri Island, Sea of Japan. *Mar Biol* 139:361-371.

Verbeek MEM, Drent PJ, Wiepkema PR (1994) Consistent individual-differences in early exploratory-behavior of male Great tits. Anim Behav 48:1113-1121.

Watanuki Y (1987) Inter- and intra-specific differences in feeding habit in *Laridae*. Ph.D. Thesis, Hokkaido-University, Hokkaido, Japan. (in Japanese)

Watanuki Y (1992) Individual difference, parental care and reproductive success in

    Slaty-backed gulls. Condor 94:159–171.

While GM, Isaksson C, McEvoy J, Sinn DL, Komdeur J, Wapstra E, Groothuis TGG.

    (2010) Repeatable intra-individual variation in plasma testosterone

    concentration and its sex-specific link to aggression in a social lizard. Horm

    Behav 58:208-213.

Wilson ADM, Whattam EM, Bennett R, Visanuvimol L, Lauzon C, Bertram SM (2010)

    Behavioral correlations across activity, mating, exploration, aggression, and

    antipredator contexts in the European house cricket, *Acheta domesticus*. Behav

    Ecol Sociobiol 64:703-715.

Wilson DS (1998) Adaptive individual differences within single populations. Philos T

    Roy Soc B 353:199–205.

Wolf M, van Doorn GS, Leimar O, Weissing FJ (2007) Life-history trade-offs favour

    the evolution of animal personalities. Nature 447:581-584.

Figure legends

**Fig. 1** Differences in the proportion of territorial attendance (a) and the frequency of territorial defense (b) between non-aggressive (○) and aggressive anti-predator defenders (●) in male Black-tailed Gulls in 2007 and 2008. Error bar and number indicates standard error and sample size, respectively. *and** indicates significant (p<0.01) differences between aggressive and non-aggressive anti-predators, and †indicates significant (p<0.01) differences between years.

**Fig. 2** Differences in the foraging trip duration (a) and the proportion of feeding sessions (the number of feeding sessions / the number of returning to the nest from foraging) (b) between non-aggressive (○) and aggressive anti-predator defenders (●) in male Black-tailed Gulls in 2007 and 2008. Error bar and number indicates standard error and sample size, respectively. * indicates significant (p<0.01) differences between aggressive and non-aggressive anti-predators, and ‡ indicates significant (p<0.01) differences between years. Interaction between behavioral trait and year (i.e. aggressiveness×year) was also significant (p<0.05).

**Fig. 3** Differences in the frequencies of attempts to copulate with mates (a) and with non-mates (b), between non-aggressive (○) and aggressive anti-predator defenders (●) in male Black-tailed Gulls in 2008. Error bar indicates standard error. * indicates significant (p<0.01) differences between aggressive and non-aggressive anti-predators.
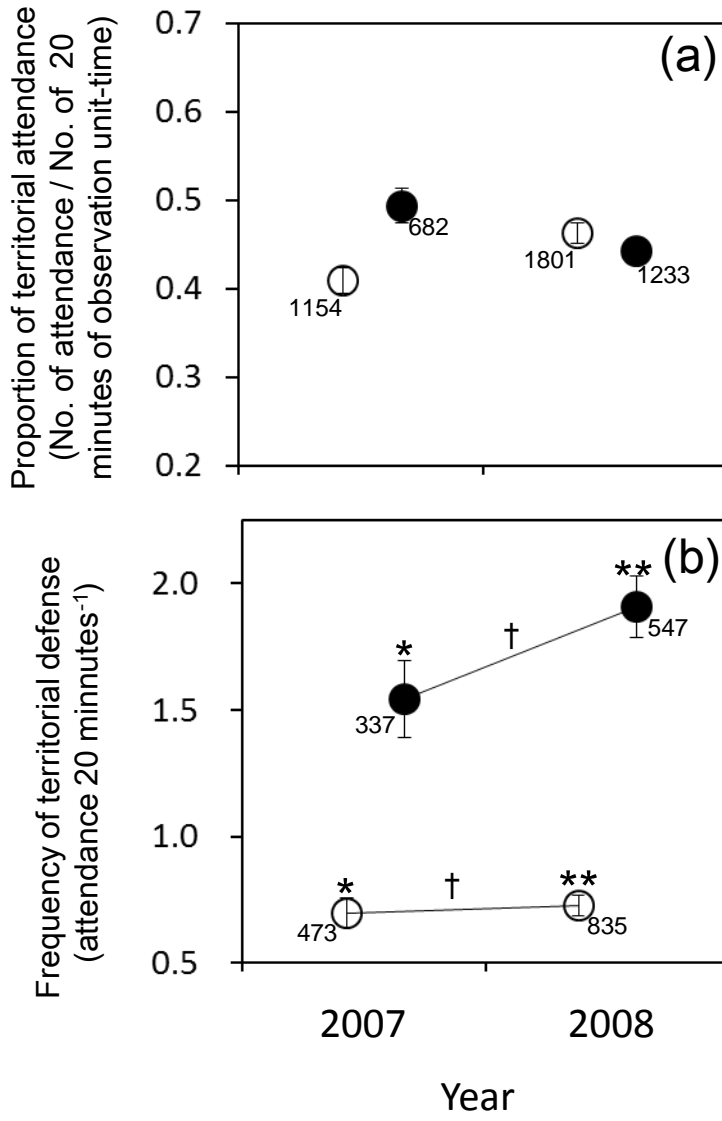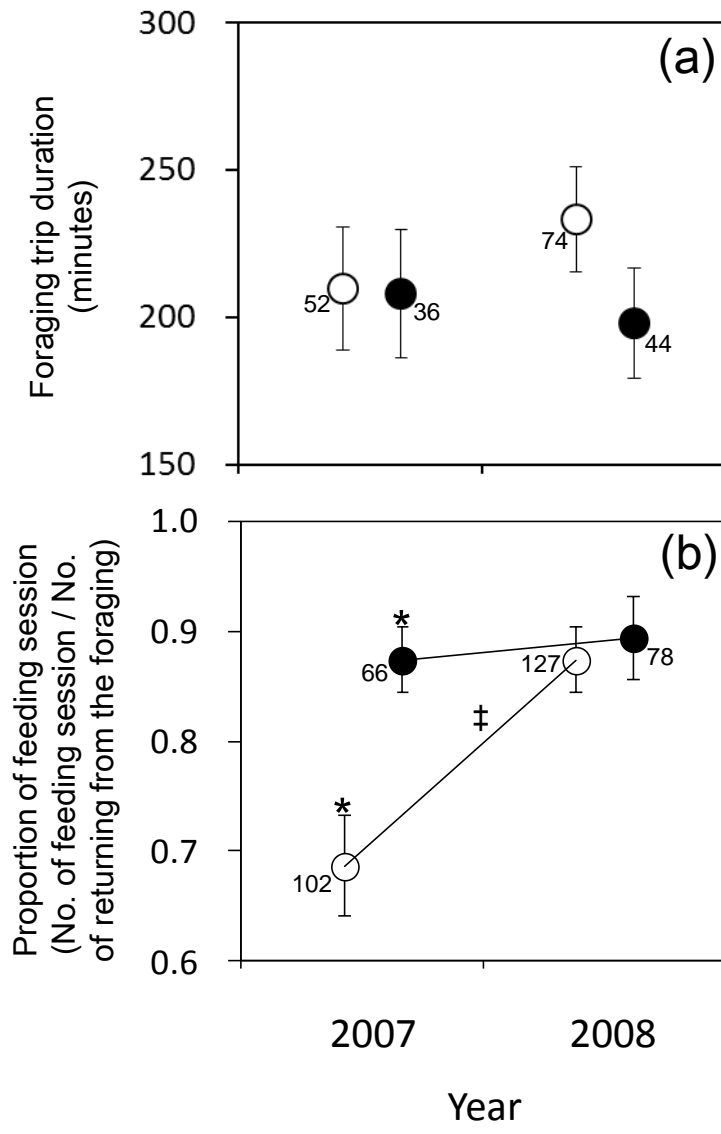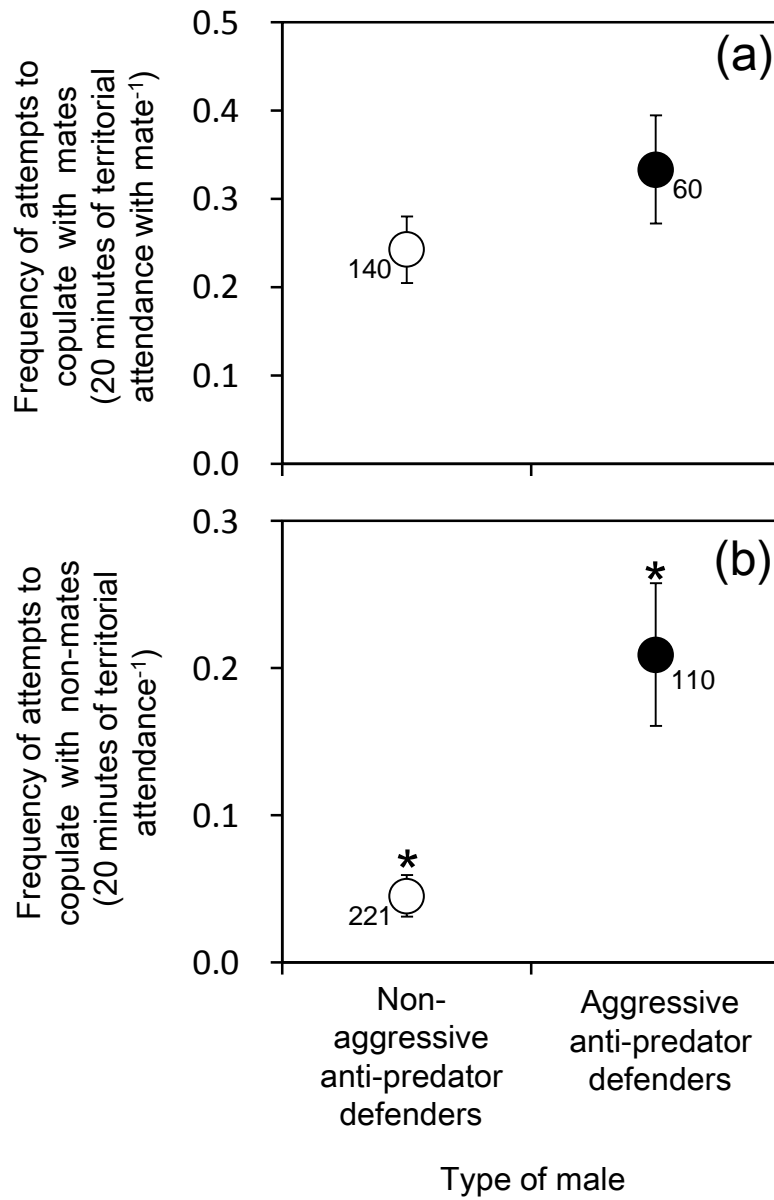
Fig.1

Fig.2

Fig.3

Table 1. Within-year repeatability (a) and between-years repeatability (b) of anti-predator aggressiveness in male Black-tailed Gulls, and of whether an anti-predator aggressive or a non-aggressive defenders, respectively. $N_{(2, 3, 4)}$ indicates numbers of individuals for which the intensity of nest defense was measured twice, three times, and four times in a year.

(a) Within-year repeatability

| Year | Proportion of consistent individuals in defense (%)* | Repeatability ($r$) ±SE | $N_{(2, 3, 4)}$ | $p$ |
|---|---|---|---|---|
| 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-years repeatability

| Year | Proportion of consistent individuals in defense (%)** | Repeatability ($r$) ±SE | N | $p$ |
|---|---|---|---|---|
| 2007-2008 | 100 | 0.99 ±0.02 | 20 | <0.001 |

*Proportion of individuals being the first defender in every decoy presentation or never being the first defender within a year.

**Proportion of individuals being an anti-predator aggressive or a non-aggressive defender in both years.

Table 2. The effect of individual behavioral trait (whether aggressive or non-aggressive defendrs), year, and the interaction on (a) proportion of territorial attendance and (b) territorial defense in male Black-tailed Gulls. GLMM results.

| Dependent variable | Fixed effect* | Parameter estimate | SE | $\chi^2$ | P |
|---|---|---|---|---|---|
| (a) Territorial attendance† | Behavioral trait | 0.164 | 0.248 | 0.001 | 0.99 |
| (N=4870) | Year | -0.133 | 0.158 | 0.67 | 0.41 |
| | Behavioral trait × Year | 0.009 | 0.205 | 0.002 | 0.96 |
| (b) Territorial defense‡ | Behavioral trait | 0.600 | 0.282 | 8.03 | <0.01 |
| (N=2192) | Year | 0.480 | 0.151 | 10.0 | <0.01 |
| | Behavioral trait × Year | 0.204 | 0.169 | 1.43 | 0.23 |

† Whether individual attend at the breeding territory (1) or not (0) for each 20 minutes of observation-unit-time, and assigned for binomial distribution (logit link function).

‡ Frequency for each 20 minutes of territorial attendance, and assigned for Poisson distribution (log link function).

* Parameter estimates were calculated when non-aggressive defenders and 2007 were coded as 0, and aggressive defenders and 2008 as 1, respectively.

Table 3. The effect of individual behavioral trait (whether aggressive or non-aggressive defendrs), year, and the interaction on foraging trip duration in male Black-tailed Gulls. GLMM results.

| Dependent variable | Fixed effect* | Parameter estimate | SE | $\chi^2$ | P |
|---|---|---|---|---|---|
| Foraging trip duration† | Behavioral trait | 0.00004 | 0.00069 | 0.001 | 0.99 |
| (N=206) | Year | -0.00048 | 0.00055 | 0.001 | 0.99 |
| | Behavioral trait × Year | 0.00072 | 0.00091 | 0.59 | 0.44 |

† Assigned for gamma distribution (log link function).

* Parameter estimates were calculated when non-aggressive defenders and 2007 were coded as 0, and aggressive defenders and 2008 as 1, respectively.

Table 4. The effect of individual behavioral trait (whether aggressive or non-aggressive defenders), year, and the interaction on proportion of feeding session in male Black-tailed Gulls. GLMM results.

| Dependent variable | Fixed effect* | Parameter estimate | SE | $\chi^2$ | P |
|---|---|---|---|---|---|
| Feeding session† | Behavioral trait | 2.769 | 1.077 | 7.24 | 0.007 |
| (N=373) | Year | 1.217 | 0.369 | 11.31 | <0.001 |
| | Behavioral trait × Year | -1.319 | 0.669 | 4.00 | 0.045 |

† Whether male fed to chicks (1) or not (0) for each arrival to the nest from foraging, and assigned for binomial distribution (logit link function).

* Parameter estimates were calculated when non-aggressive defenders and 2007 were coded as 0, and aggressive defenders and 2008 as 1, respectively.