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ABSTRACT

The physiological state of parent birds combined with the value of their clutch may affect the intensity of their nest defense. In colonially breeding birds nest defense intensity may also be affected by the behavior of neighbors. We investigated individual variation in the intensity of nest defense among colonial Black-tailed Gulls *Larus crassirostris* in two years. Only 30-40% of males attacked a decoy of an egg predator (crow), and the other males and females rarely attacked. Males attacking the decoy had higher levels of plasma testosterone than males that did not attack. Each male's, but not female's, nest defense intensity was consistent throughout the incubation period and also across years. The intensity was not related to egg-laying date, clutch size, or age of offspring. The intensity was likely to be higher when individuals had one or more neighbors, representing higher nest defense intensity in the year where gulls had larger number of adjacent neighboring nests (5.23 nests), but this trend was not observed in the year where they had smaller number of the neighboring nests (3.73 nests). Thus, in addition to testosterone levels, behavior of neighbors also influences the intensity of nest defense.

INTRODUCTION

Among birds, defending nests against predators is fundamental to increasing reproductive success; the level of such defense is hypothesized to be an outcome of the trade-off between the increase in offspring survival and the risks of injury to the parents (reviewed by Montgomerie and Weatherhead 1988; Caro 2005). The intensity of nest defense is affected by the size and age of the clutch or brood, timing of breeding, and sex, age, or quality of the parents. Males (Reid and Montgomerie 1985), parents having a larger number of eggs or chicks (Greig-Smith 1980; Wallin 1987; Brunton 1990), and parents having good body condition (Lessells 1991), tend to engage in higher intensities of nest defense.

Nest defense intensity may also be related to individual variation in aggressiveness (Hollander et al. 2008) that may be consistent throughout the breeding season and across years (reviewed by Groothuis and Carere 2005). Aggressiveness is moderately heritable (Drent et al. 2003; van Oers et al. 2005) and often correlates with hormonal levels (e.g. Testosterone and Corticosterone) (Koolhaas et al. 1997; Cockrem 2007; Kralj-Fiser et al. 2007).

In colonially breeding birds, nest defense intensity may be also affected by the behavior of neighbors. Breeding neighbors in a colony are assumed to share predation risks and defense duties (Burger and Gochfeld 1991). Therefore, the costs and benefits of individuals defending their own nests should vary also with the levels of defense of the neighbors (Allaine 1991; Brown and Brown 1996). Studies of these neighbor effects, during mobbing and direct attacks at predators, involving high costs and risks for parents, are scarce (but see Winkler 1994; Arroyo et al. 2001).

Black-tailed Gulls *Larus crassirostris* nest colonially on gentle slopes on

Rishiri Island where vegetation or rocks provide moderate cover. They lay clutches of 1-3 eggs (Kazama 2007); however Jungle Crows *Corvus macrorhynchos* take 30% of their eggs (Kazama 2007). Parent gulls typically defend their nests aggressively against the crows using intimidating actions (by: opening the bill and wings, body striking, or swooping) (Kazama 2007; Kazama and Watanuki 2010). There is considerable individual variation among parent gulls in this nest defense intensity affecting its frequency and duration (Kazama and Watanuki 2010). Factors affecting this individual variation in nest defense intensity were examined under extremely high levels of predation risk, where Jungle Crow attack levels were manipulated to average 5-22 times normal attack rates by the placement of artificial nests containing unguarded eggs at the perimeter of the gull colony (Kazama and Watanuki 2010), but not under natural conditions.

In this study, in order to establish which factors affect individual variation in nest defense intensity among parent gulls, firstly we examined whether individual's nest defense intensity was consistent both within- and between-years. Secondly, the effects of sex, size and age of clutch, timing of egg-laying, and behavior of neighbors, on nest defense intensity were examined. Finally, correlations between individual variation in nest defense intensity and hormonal state (plasma testosterone level) was also examined.

METHODS

Study area and period

The study was conducted from 20 April to 10 July 2007 and 2008 on Rishiri Island situated in the Sea of Japan at 45°14'N, 141°09'E, 40 km off northern Hokkaido, Japan.

A study site of 0.19 ha and including 157 nests in 2007 and 107 nests in 2008 was established in a sub-colony at Oiso. Nesting microhabitat and location may affect the potential vulnerability of nests to predation (Brunton 1990; Galeotti et al. 2000) and hence parental nest defense behavior. In Black-tailed Gulls, nesting position (<4 m from edge of the breeding area or not) and vegetation heights surrounding the nest-sites affect the risk of egg predation (Kazama 2007). Therefore, we established the study area in a small and narrow sub-colony where all nests were <4 m from edge of the breeding area, and we also cut back the vegetation around the nests every 1–2 days to maintain its height shorter than 15 cm, so as to control for uniform nest potential vulnerability to predation. Nest contents were checked every 1 or 2 days. All the nests in the study site were mapped and marked with numbered stakes immediately after eggs were laid.

Identifying individuals and blood sampling

To identify sex of all individual gulls within the study site in each year (314 gulls in 2007 and 214 in 2008), we observed at least once courtship feeding or copulation behavior (males courtship feed to mates and mount on mates) before egg-laying for each pair in each year. Thus we could completely identify sex of all individuals within the study site. Further, to facilitate individual identification of the gulls, black hair dye (Bigen hair color, containing aminophenol and stearic acid as major ingredients; Hoya Co., Ltd., Nagoya, Japan) was used in each year. During the incubation period, dyed stones or leaves were placed in all the nest cups within the study site so that the dye would mark the breast or neck of either the male or female parent, whichever returned to incubate the eggs first.

To identify individuals from year to year, 34 males (22% of all the males within

the study site) in 2007 were captured by box- or line-trap, and these birds were banded with numbered plastic and metal rings. In 2008, 26 of all the males captured and banded in 2007 returned and nested at the same nest-site in 2007 (a rate of return was 76.4%). Although nest-site and mate fidelity of *Larids* across years would be high (Blokpoel and Courtney 1980; Naves et al. 2006), all the gulls not attached the rings were regarded as another individuals between years, even if they returned to the nest-sites where they nested in previous year. In 2008, 30 males were captured (26 males of them were re-captured). Head lengths of all captured males were measured to the nearest 0.02 mm with calipers (D30TN, Mitutoyo Co., Ltd., Kawasaki, Japan) following the procedure described in Bosch (1996).

As plasma testosterone levels of male Black-tailed Gulls change with the elapsed day from first egg-laying (Kazama et al. 2008), 1.0 ml blood was taken from the brachial wing veins of 24 males in 2007 and 12 males in 2008 captured within four to six days after the date of first egg-laying (blood was taken with an EDTA-rinsed syringe within two minutes of capture). The mean total handling time (from capture to release) of bled gulls was nine minutes ($N=36$). After centrifugation at $2000\times g$ for 10 minutes, plasma was stored at -30°C .

No behavioral changes resulting from color marking, such as an increase in susceptibility of marked birds to predation or territorial attack by other birds, were observed. No marked birds abandoned their nests and no marked pairs stopped incubating their clutches during the study periods. Thus, neither handling, nor manipulation, harmed the gulls.

Nest defense intensity

To control for the proximity and approach speed of predators to nests, and the weather and wind conditions, all of which may influence the defense response (Gilchrist et al. 1998), we exposed individual gulls 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) from 13:00-17:00 on clear and calm days. The decoy was placed at ground level 1.5m from the nearest nest to the decoy and covered with a cloth for more than 30 minutes before beginning the presentation so as to allow the gulls to calm down following their disturbance by researchers. The decoy was exposed to the gulls for two minutes by pulling on a line attached to the cloth to remove it. No more than four presentations were conducted in a day for nests within 10 m of one another. The decoy was exposed to gulls more than 3 days intervals if the decoy was exposed repeatedly to the same gulls within a year. During each presentation gulls were incubating and their mates were away from their nests (single gull stayed each nest). During decoy presentations no Jungle Crows attacked gull nests within the study site.

Since distance between gulls and the predator does not affect defense response in Black-tailed Gulls (Kazama and Watanuki 2010), we recorded responses of three to six gulls nesting within <2.5 m radius of the decoy at once in a decoy presentation from a blind situated five meters from the study site. During the decoy presentation, all the gulls within <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. Since all gulls within <2.5m radius of the decoy responded to the decoy (i.e. stopped incubation and stood up), all the gulls could be stimulated by the decoy. 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 by crows, the first gulls to

attack the crow drove it away effectively and quickly (several seconds), we have called these “first defenders”. Although only rarely (<1% of all defense) did other gulls join in the nest defense against Jungle Crow (Kazama and Watanuki 2010), sometimes two or three gulls defended against the decoy in this study because the decoy remained the ground during two minutes decoy presentation. Thus, the one or more gulls attacking the decoy once or more during the two minutes presentation were defined as “first defenders” in this study.

In 2007, we collected 151 records of the defense intensity from 58 males (including 34 captured-males) and 39 females. In total 39 presentations, the intensities of nest defense (the first defender or not) were measured once each for 17 males and 20 females, twice each for 35 males and 12 females, three times each for 6 males and 6 females, and four times each for one female. In 2008, we collected 177 records of defense intensity from 58 males (including 26 re-captured-males) and 46 females. In total 46 presentations, the intensities of nest defense were measured once each for 30 males and 25 females, twice each for 18 males and 14 females, three times each for 7 males and 4 females, four times each for 3 males and 2 females, and five times each for one female. For 26 re-captured-males, nest defense intensity was measured repeatedly in both 2007 and 2008.

Testosterone assay

Plasma testosterone levels were measured by enzyme immunoassay using a commercial kit (Correlate-EIA, Assay designs ltd., Miami). The cross-reactivity of this kit with 19-hydroxytestosterone and dihydrotestosterone was 14.46% and <0.001% respectively (provided by Assay designs ltd.). The minimum detectable level of plasma testosterone

was 0.0029 ng/ml, and the standard curve range was 0.008-2.0 ng/ml. For each plasma sample, 100 μ l was assayed in duplicate. The samples collected in 2007 and 2008 were assayed in separate series. The intra-assay coefficients of variation were 1.1% in 2007 and 2.3% in 2008, and the cumulative inter-assay coefficients of variation were 2.2% in 2007 and 4.4% in 2008.

Statistical analysis

Between year differences in the date of first egg-laying, clutch size, and the number of neighbor nests (number of adjacent neighbor nests within <1.5m radius) were examined using Linear Mixed Models (LMM) where year was included as a fixed effect. As 26 re-captured-males were observed repeatedly in 2007 and 2008, nest identity was included as a random effect in the models to avoid pseudo-replication.

To examine individual consistency of nest defense intensity within-year and between-years, the repeatability (r) of the intensity 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 (Lessells and Boag 1987), and was calculated for binomial data following Nakagawa and Schielzeth (2010). Standard error and statistical significance of repeatability was calculated following Becker (1984), and Nakagawa and Schielzeth (2010), respectively. Within-year repeatability was calculated for gulls where nest defense intensity was measured more than twice within a year (41 males and 18 females in 2007 and 28 males in 2008). The repeatability for females in 2008 could not be calculated because no females, of which the intensity of nest defense was measured more than twice within the year (21 females), became the first defender. Males that were first defenders at least once in each year were defined as “aggressive

defenders” and the others were called “non-aggressive defenders”. Between-years repeatability was calculated as whether the male was consistently aggressive or non-aggressive defender across years, and calculated for 26 re-captured-males.

We examined factors affecting nest defense intensity using Generalized Linear Mixed Models (GLMM) with binomial distributions for nest defense intensity of individual gulls in each decoy presentation (the first defender or not), for each year separately. The models contained sex, clutch size, first egg-laying date, clutch size, age of first egg (elapsed days from first egg-laying date), and the intensity of nest defense by neighbors, which is a 0/1 value (gulls having at least one first defender neighbor in the decoy presentation had a value of one, while the others had a value of zero) as fixed effects, and individual identity as a random effect. We used the 151 records of nest defense intensity from 2007 and the 177 records from 2008 in the analyses.

The effect of plasma testosterone levels on the intensity of nest defense was examined in males (16 in 2007 and 8 in 2008) using GLMM with binomial distribution, where aggressive (1) or non-aggressive (0) defender was a dependent variable, plasma testosterone level and year were fixed effects, and individual identity was a random effect. To normalize the plasma testosterone levels measured using different series of assays, we applied Z-score transformations in each year. To examine the effects of body size (relative head length (mm; measured size – mean size) on the intensity of nest defense in males, we fitted Generalized Linear Model (GLMs) with binomial distributions including body size and year as independent variables. Among *Larids*, skeletal size is considered suitable as an index of body size because individual variation in skeletal size is greater than in other parts of the body (such as wing length) (Croxall 1995). Since above two analyses included data from different years, year was included

as independent variable into those analyses to control for the effect of year.

All analyses of this study were performed using R ver. 2.12.0 (R Development Core Team 2010).

RESULTS

Breeding biology in 2007 and 2008

The mean first egg-laying date (elapsed days from 1 May \pm SD) in 2007 (4.39 ± 4.01 , $N=157$) did not differ significantly from that in 2008 (4.21 ± 3.81 , $N=107$; LMM, $t=-0.85$, $p=0.40$). Nor did mean clutch size (\pm SD) in 2007 (2.25 ± 0.53 , $N=157$) differ significantly from that in 2008 (2.20 ± 0.57 , $N=107$; LMM, $t=-0.78$, $p=0.44$). However, the mean number of neighbor nests (number of adjacent neighboring nests within $<1.5\text{m}$ radius \pm SD) in 2007 (5.23 ± 2.00 , $N=157$) was significantly greater than in 2008 (3.73 ± 1.66 , $N=107$; LMM, $t=-6.67$, $p<0.001$).

Repeatability of nest defense intensity

The intensity of nest defense of males was highly repeatable within a year in both 2007 and 2008, but not of females (Table 1a). In 2007 34% of males (20/58 individuals) and 5% (2/39) of females were categorized as aggressive defenders, while in 2008, 41.4% (24/58) of males and 8.7% (4/46) females were so categorized. Whether males were aggressive or non-aggressive defenders was highly repeatable between years (Table 1b).

Factors affecting variation in nest defense intensity

Males were more likely to be the first defender than female in both the years (Table 2 and Table 3). When the decoy was exposed gulls with first defenders among their

neighbors were more likely to be a first defender than those without such neighbors in 2007, though this was not the case in 2008 (Table 3, Fig. 1). Neither first egg-laying date, clutch size, nor age of first egg affect the intensity of nest defense in both the years (Table 3).

Effect of testosterone levels and body size

The mean level of male plasma testosterone (ng/ml \pm SE) was 0.162 ± 0.02 (range: 0.06-0.37, N=24) in 2007 and 0.187 ± 0.06 (0.06-0.67, N=12) in 2008. Males having higher levels of normalized plasma testosterone were more likely to be aggressive defenders (GLMM, Estimate \pm SE= 1.38 ± 0.66 , $Z=2.10$, $p=0.036$, $N=24$) without year effect (Estimates \pm SE= -0.09 ± 1.12 , $Z=-0.08$, $p=0.933$, $N=24$). Relative head length, a measure of body size, did not significantly correlate with male aggressiveness (aggressive or non-aggressive defenders; GLMs, Estimate \pm SE= 0.26 ± 0.19 , $Z=1.41$, $p=0.16$, $N=40$) without year effect (Estimate \pm SE= -0.38 ± 0.93 , $Z=-0.41$, $p=0.68$, $N=40$).

DISCUSSIONS

Previous studies have predicted that levels of nest defense should be regulated in relation to the size and age of the clutch and the timing of egg-laying (Montgomerie and Weatherhead 1988; Caro 2005). In Black-tailed Gulls, however, the intensity of nest defense of males was highly repeatable over time within a year and between years, and was related to plasma testosterone levels rather than the size and age of the clutch, the timing of egg-laying, or body size (head length). Further, females rarely defended their nests. These suggest that the level of plasma testosterone is a dominant factor constraining the intensity of nest defense in Black-tailed Gulls. In *Larids* during

breeding season plasma testosterone levels of males are 2-15 times higher than those of females (Wingfield and Farner 1993).

In birds, genetic or maternal effects, and age or social status are assumed to control individual variation in plasma testosterone levels (Kempnaers et al. 2008). In male Black-tailed Gulls non-aggressive defenders rarely became aggressive defenders in the next year (Table 1b), indicating that the plasma testosterone level and the intensity of nest defense were controlled by certain long-term (at least over two years) consistent factors, such as genetic or maternal effects. Since age of males was unknown in our study, we also could not rule out the age effect on the level of plasma testosterone and the intensity of nest defense in long-lived Black-tailed Gulls (over 20 years in maximum, Narita and Narita 2004).

Parents of colonially breeding Montagu's Harriers *Circus pygargus* reduce the intensity of nest defense if their neighbors participate in group defense (Arroyo et al. 2001). In contrast, parent Black-tailed Gulls with neighbors showing higher levels of defense, defended their nests more intensively. One possible explanation for our results is the "responsive amplifier" (Winkler 1994). In another colonial species, the Tree Swallow *Tachycineta bicolor*, parents use the intensity of nest defense of close neighbors as a reliable indicator of the threat of a predator to their own nest, and the intensity of nest defense increases if an individual has neighbors showing higher levels of defense (Winkler 1994). Another possible explanation is reciprocation. An egg-predator, such as the Jungle Crow, may attack the same area repeatedly during the incubation period at a gull colony (Kazama 2007; Kazama and Watanuki 2010). Therefore, neighbors of a first defender were likely to cooperate as a first defender (really a "second defender") in expectation of reciprocation if their own nests were

subsequently threatened. In 2008, however, the intensity of nest defense among Black-tailed Gulls did not correlate with that of their neighbors. Among Tree Swallows, the probability of parents participating in group defense was higher when neighboring nests were more closely adjacent (Winkler 1994). In this study of gulls, the number of adjacent neighbour nests was smaller in 2008 than in 2007.

Only about 30-40% of male Black-tailed Gulls showed aggressive defense consistently over time. Among birds, anti-predator defense is associated with time and energy costs, and injury risks (Dugatkin and Godin 1992). High levels of testosterone can cause an immunosuppressive effect (Bederovsky and Del Rey 1996), decrease survival (Nolan et al. 1992), and reduce parental care (Ketterson et al. 1992, Alonso-Alvarez 2001). Furthermore, aggressive defenders reduce the risk of egg predation for their neighbors' nests as well as their own (Kazama and Watanuki 2010). Hence aggressive defenders partly support an increase in the reproductive success of their potential competitors. These suggest that the balance between the costs and benefits of anti-predator nest defense would differ between aggressive and non-aggressive defenders. Further study of the reproductive advantages of aggressive defenders is necessary to examine the adaptive significance of aggressive nest defense in this study species.

In conclusion, the intensity of nest defense by Black-tailed Gulls was not regulated based on size and age of clutch, timing of egg-laying, or body size, but may be affected by the intensity of nest defense of their neighbors in addition to their plasma testosterone levels.

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Figure legend

Fig. 1 Comparisons of the probabilities of individual Black-tailed Gulls being a first defender between those having neighboring first defenders and those without, when a decoy of a crow was presented in 2007 and 2008. Numbers above the bars indicate the number of records. Significant p -values were obtained from GLMM (see Table 3).

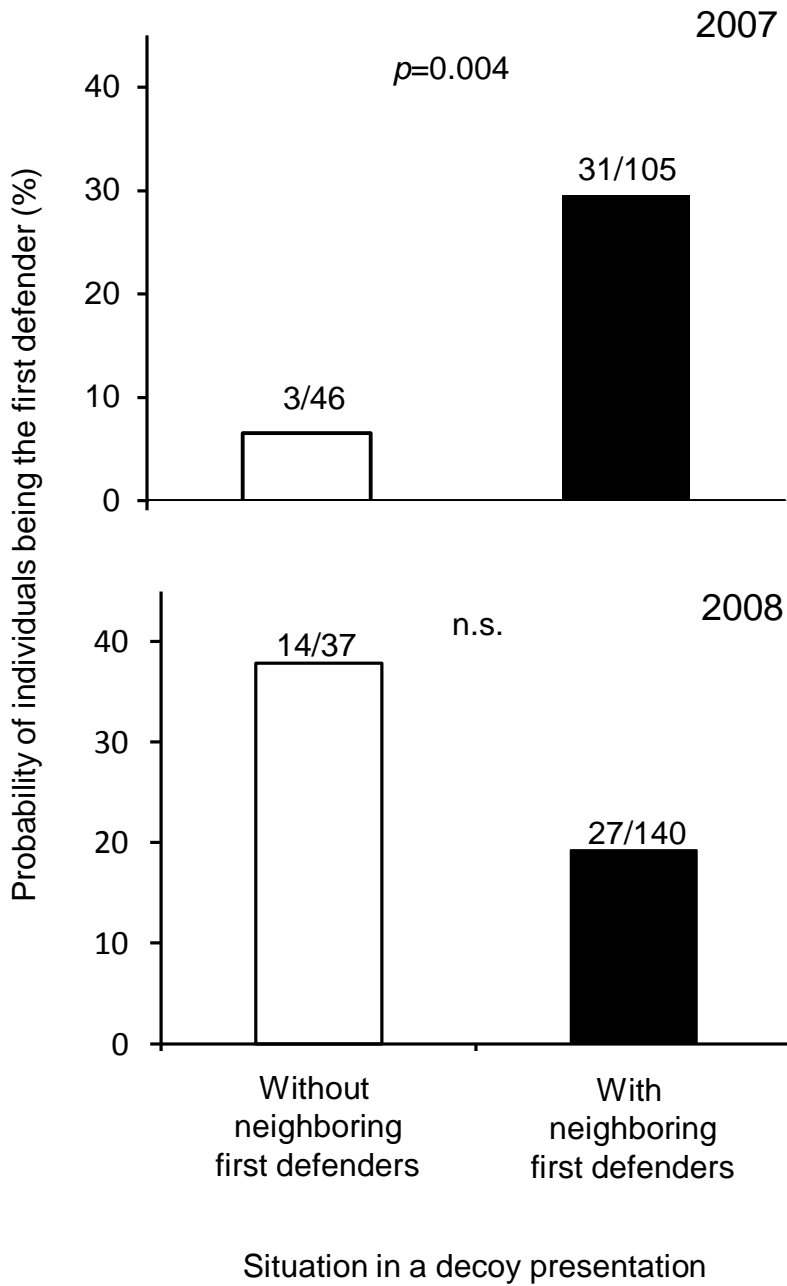


Fig.1

Table 1 Within-year repeatability (a) and between-years repeatability (b) of the intensity of nest defense in Black-tailed Gulls.

(a) Within-year repeatability

Year	Sex	Proportion of consistent individuals in defense (%)*	Repeatability (r) \pm SE	p	$N_{(2, 3, 4)}\ddagger$
2007	Male	78.0	0.34 \pm 0.13	0.004	35, 6, 0
	Female	61.1	0.00 \pm 0.18	0.99	11, 6, 1
2008	Male	89.3	0.77 \pm 0.06	<0.001	18, 7, 3
	Female	-	-	-	-

(b) Between-years repeatability \ddagger

Year	Sex	Proportion of consistent individuals in defense (%)**	Repeatability (r) \pm SE	p	N
2007-2008	Male	92.3	0.83 \pm 0.06	<0.001	26

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

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

\ddagger Calculation as the repeatability of whether a gull was an aggressive or non-aggressive defender across years.

**Proportion of individuals being aggressive defender or non-aggressive defender both in the years.

Table 2 Probability % of being the first defender in a decoy presentation in 2007 and 2008.

Year	Males*	Females*
2007	28.1 (89)	14.5 (62)
2008	37.4 (99)	5.1 (78)

*Number in parenthesis is the number of records of the nest defense intensity.

Table 3 Factors affecting the intensity of nest defense of Black-tailed Gulls to egg predator's decoy (crows) in 2007 and 2008.

Fixed effects	Estimate	SE	Z	<i>p</i>
2007, <i>N</i> =151				
Sex	-1.429	0.537	-2.66	0.008
Clutch size	0.302	0.496	0.61	0.54
First egg-laying date	-0.079	0.083	-0.95	0.34
Age of first egg	0.063	0.043	1.48	0.14
Neighbor's behavior*	2.113	0.742	2.85	0.004
2008, <i>N</i> =177				
Sex	-3.186	0.952	-3.35	0.001
Clutch size	0.337	0.689	0.49	0.62
First egg-laying date	-0.114	0.123	-0.93	0.35
Age of first egg	0.039	0.087	0.45	0.65
Neighbor's behavior*	-0.898	0.681	-1.32	0.19

*Whether individual had one or more neighboring first defenders or not when decoy was presented.