

Corticosterone facilitates begging and affects resource allocation in the black-legged kittiwake

Alexander S. Kitaysky,^a John C. Wingfield,^a and John F. Piatt^b

^aDepartment of Zoology, 24 Kincaid Hall, Box 351800, University of Washington, Seattle, WA 98195, USA, and ^bAlaska Biological Services Center, U.S. Geological Survey, 1011 E. Tudor Road, Anchorage, AK 99503, USA

Parent black-legged kittiwakes (*Rissa tridactyla*) and their dependent chicks respond to food shortages by increasing circulating levels of corticosterone. To examine the behavioral significance of corticosterone release, we experimentally increased levels of circulating corticosterone in parents and chicks up to the levels observed during food shortages. We found that corticosterone-implanted chicks begged more frequently than sham-implanted controls. Corticosterone-implanted chicks in broods of two begged more frequently than singletons. Parent kittiwakes then responded to the increase in corticosterone levels in their chicks by increasing chick-feeding rates. However, feeding rates were not different among corticosterone-implanted chicks in broods of two and singletons. We also found that corticosterone-implanted parents spent more time away from the nest—perhaps foraging—and less time brooding/guarding chicks than sham-implanted controls. Untreated mates of the corticosterone-implanted bird did not compensate for the change in their partner's behavior; consequently, chicks were left unattended about 20% of the time compared to 1% at the control nests. However, corticosterone-implanted parents did not decrease their chick-feeding rates. Our findings suggest two functional implications of the increased corticosterone secretion during food shortages in the black-legged kittiwake: it facilitates begging in chicks, and it affects time allocated by parents to guarding young at the nest. Thus, release of corticosterone might provide a mechanistic link between physiological condition and behavioral interactions among adults and their young. *Key words*: begging, corticosterone, food stress, kittiwakes, parent-offspring conflict, *Rissa tridactyla*, seabirds. [*Behav Ecol* 12:619–625 (2001)]

Nest-dependent chicks communicate their needs by begging, and parents use this information to adjust their investment in food provisioning. Parent-offspring conflict theory predicts that chicks should be selected to solicit a greater investment from their parents than the parents have been selected to provide (Trivers, 1974). Alternatively, signal selection theories suggest that begging reliably conveys chick nutritional needs and that parents respond accordingly (Godfray, 1991, 1995a,b; Zahavi, 1987). The intensity of chick begging increases with food deprivation (e.g., Cotton et al., 1996; Iacovides and Evans, 1998; Kilner, 1995; Stamps, 1993), and, at least in some species, parents provision more in response to elevated begging (Henderson, 1975; Leonard and Horn, 1996; Price and Ydenberg, 1995). Although the relationship between hunger levels and chick begging seems well established, the causal mechanism(s) regulating parent-offspring feeding interactions during food shortages is not established. Finding a mechanistic link between hunger and changes in behavior is essential to assessing theoretical models and, eventually, to better understanding the evolution of chick-begging behavior and parental provisioning strategies.

When food resources are limiting, long-lived parent birds are expected to allocate available resources to body maintenance rather than to reproduction (Cody, 1966). Evidence is accumulating that a decision of parents about the allocation of available resources might be based on their physiological condition (Chaurand and Weimerskirch, 1994; Ricklefs and

Schew, 1994; Weimerskirch et al., 1994). Long-lived birds can accumulate fat as energy reserves for self-maintenance during reproduction (Drent and Daan, 1980). As fat reserves are depleted, parents should rely more on amino acid metabolism (mostly from muscle protein; Cherel et al., 1988), which is stimulated by secretion of corticosterone, a steroid hormone released by the adrenal glands in response to stress (Veiga et al., 1978).

In adults, increased plasma levels of corticosterone facilitate foraging behavior, trigger irruptive migration, and mobilize stored energy resources to fuel increased locomotory activities (Astheimer et al., 1992; Bray, 1993; Wingfield et al., 1997). These behavioral responses can improve adult survival during food shortages (Astheimer et al., 1992). Increased secretion of corticosterone might also change the allocation of available resources between body maintenance and reproductive processes to facilitate the survival of affected individuals (Silverin, 1986; Wingfield and Silverin, 1986; Wingfield et al., 1997, 1998).

In contrast to adult birds, nest-bound chicks are limited in their behavioral responses to food-related stress. A hungry chick can compete with nest mates and increase its share of parental resources at the expense of siblings. A hungry chick can also intensify its begging for food from a parent, which would respond by feeding a chick more frequently. Therefore, chick behavioral strategies during food shortages may reflect both the selective pressure of competition between siblings and chick nutritional requirements (but see Cotton et al., 1996). Experimental studies have shown that in nest-bound chicks, food shortages are associated with depleted fat reserves and an increase in circulating levels of corticosterone (Kitaysky et al., 1999a; Nunez-de la Mora et al., 1996), though little is known about behavioral responses of chicks to increased corticosterone.

Address correspondence to A. Kitaysky. E-mail: kitaysky@u.washington.edu.

Received 1 May 1999; revised 10 November 2000; accepted 9 December 2000.

© 2001 International Society for Behavioral Ecology

In this study we examined the behavioral responses of black-legged kittiwakes (*Rissa tridactyla*) to increased corticosterone. Black-legged kittiwakes are colonial, cliff-nesting gulls with a maximal brood size of three, and their chicks are nearly constantly brooded or guarded at the nest by one of the parents (Braun and Hunt, 1983; Roberts and Hatch, 1993). Both sexes provision young with food throughout chick rearing; usually 5–6 weeks. Parent kittiwakes alternate their duties: while one parent is brooding chicks, another is at sea foraging for itself and collecting food for the young (Braun and Hunt, 1983). Males and females do not show differences in nest attendance or reproductive effort (Coulson and Wooller, 1984). When a foraging parent returns to the nest, a brooding parent leaves for the ocean. During good foraging conditions, this synchronized behavior results in the constant presence of one of the adults at the nest until chicks are about 34 days old (Braun and Hunt, 1983). If food supply is poor, however, parents start to leave their chicks unattended at an earlier age (Roberts and Hatch, 1993). Thus, experimentally increased levels of corticosterone might cause a kittiwake raising young chicks to increase time spent foraging at the expense of leaving chicks unattended.

In black-legged kittiwakes, a hungry chick appears to have only two behavioral options to improve its chances of survival (Braun and Hunt, 1983): either eliminate nest mates (siblicide) or intensify its begging for food. Begging behavior is probably the only form of foraging behavior available to nest-bound chicks. Because increased levels of corticosterone facilitate foraging behavior in adult birds, it is reasonable to hypothesize that experimentally increased levels of corticosterone might affect begging in nest-bound chicks.

Elsewhere we have shown that a seasonal decrease in parent kittiwake body condition is associated with a seasonal increase in their circulating levels of corticosterone (Kitaysky et al., 1999b). Furthermore, the seasonal increase in baseline levels of corticosterone is stronger among birds rearing young under poor foraging conditions compared to those breeding under favorable foraging conditions (Kitaysky et al., 1999b). We also have shown that black-legged kittiwake chicks increase circulating levels of corticosterone in response to food-related stress (Kitaysky et al., 1999a). However, the functional role of corticosterone release in regulating feeding interactions of parents and their chicks has not yet been investigated.

In the present study, we experimentally increased levels of circulating corticosterone in kittiwake parents and chicks at a food-rich colony. Our objectives were to test (1) the behavioral responses of parents and chicks to the experimentally increased circulating levels of corticosterone, (2) the behavioral responses of parents to the corticosterone-induced changes in behavior of their offspring and vice versa, and (3) the behavioral responses of intact parents to the corticosterone-induced changes in behavior of their mates.

METHODS

Study area

We carried out the experimental manipulations and behavioral observations from 24–27 July 1997 at a colony of seabirds on Gull Island in the lower Cook Inlet, Alaska, USA (59°35' N, 151°19' W). Foraging conditions were favorable for black-legged kittiwakes nesting at the colony in 1997 (Kitaysky et al., 1999b; Piatt JF et al., unpublished). The study plot consisted of a 30 × 25 m vertical wall that contained 40 active nests of black-legged kittiwakes. We monitored all nests at the study plot at 3-day intervals from the egg-laying stage to fledging of chicks. We observed birds from a blind that had been placed at the colony before kittiwakes started egg laying; at

the time of the experiment (mid-chick-rearing), birds were habituated to the presence of observers in the blind. The blind faced the study plot at a distance of about 15 m.

Experimental design

We randomly selected a total of 24 nests for 4 experimental treatments (in 2 treatments we manipulated chicks and in 2 treatments we manipulated parents). Each treatment had equal numbers of nests with one and two chicks.

Experimental manipulations with chicks

At experimental nests we implanted chicks subcutaneously with a single 25-mm silastic tube (Dow Corning) filled with crystallized corticosterone. At control nests we implanted chicks with a single 25-mm empty silastic tube. Both chicks from broods of two were treated similarly. We individually marked chicks using spots of colored dyes on the forehead and breast. This method has been used in previous experimental studies of birds and does not observably affect behavior of chicks or parents (e.g., Cotton et al., 1999). Estimated mean distances between nests within a treatment were 1.1 ± 0.52 (SD) and 1.0 ± 0.54 m for nests with corticosterone-implanted and sham-implanted chicks, respectively. The average age of corticosterone-implanted chicks (14.8 ± 3.71 [SD] days after hatching) was similar to sham-implanted chicks (15 ± 3.35 days). In this study we were not always able to distinguish between α and β chicks within a brood; therefore, we could not examine behavioral differences between siblings according to their hierarchical status.

Experimental manipulations with parents

At experimental nests we implanted one of the parents subcutaneously with two 25-mm silastic tubes filled with crystallized corticosterone. At control nests we implanted one of the parents with two 25-mm empty silastic tubes. Estimated mean distances between nests within a treatment were 1.7 ± 1.38 (SD) and 2.1 ± 0.96 m for nests with corticosterone-implanted and sham-implanted parents, respectively. Age of chicks was similar between the experimental treatments, averaging 16.3 ± 4.08 (SD) and 16.5 ± 4.37 days old for nests with corticosterone-implanted and sham-implanted parents, respectively. We individually marked each manipulated bird with a unique combination of color leg bands and spots of colored dyes on the forehead and breast.

Nest observations

We conducted observations of all nests from the blind with 8 × 40 binoculars over a 2-day period beginning 24 h after implant placement. We watched nests continuously from 0700 to 1800 h (by two observers recording simultaneously during 2-h shifts). We recorded begging rates of chicks, food provisioning rates, and nest attendance of parents. We also recorded aggression between siblings. Color markings allowed us to follow the behavior of individual birds. We defined begging rates as the number of begs per chick per hour at each nest. We defined begging as a chick solicitation (frequent vertical movements of the head accompanied by a high-pitch vocalization) for food from a parent. We considered begging series with pauses of more than 1 min as separate begging signals. We defined feeding rates as the number of feeds per chick per hour at each nest. We considered consecutive feedings that occurred more than 5 min apart as separate meals. We calculated the number of trips away from the nest performed by parents as the mean number of trips per parent per nest per 2-day study period.

After the experiment, we monitored the experimental birds until chicks fledged. In 1998 and 1999, to resight the exper-

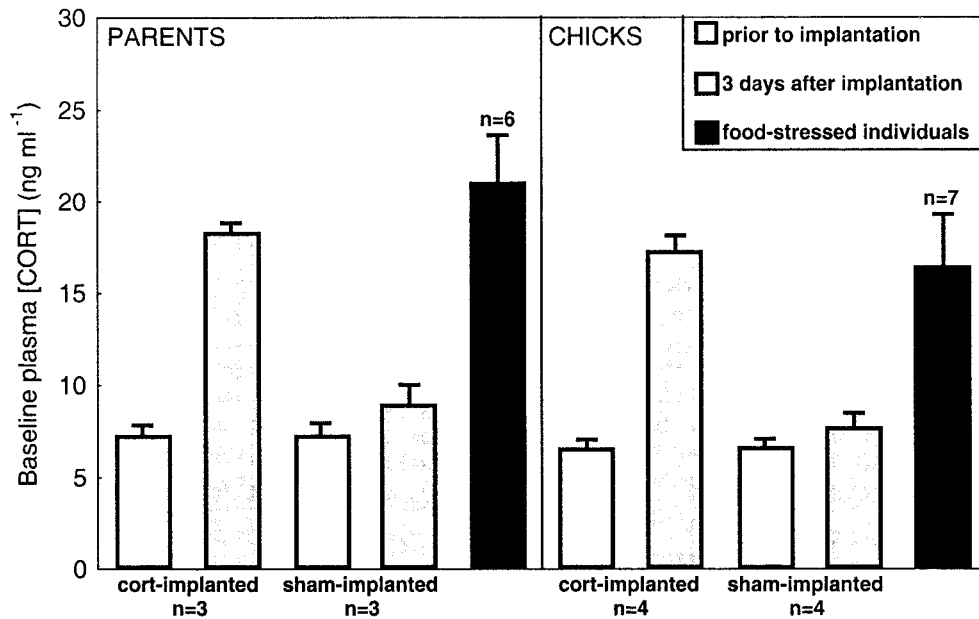


Figure 1

Effects of corticosterone (cort) implants on baseline plasma levels of corticosterone in black-legged kittiwakes (means \pm SE). Corticosterone implantation caused a significant increase in baseline corticosterone in parents (paired *t* test, $t = 58.26$, $df = 2$, $p < .001$) and chicks (paired *t* test, $t = 6.41$, $df = 3$, $p = .008$). Sham implantation did not cause a significant change in baseline levels of corticosterone in parents (paired *t* test, $t = 1.59$, $df = 2$, $p = .253$) or chicks (paired *t* test, $t = 0.64$, $df = 3$, $p = .568$). Baseline levels of food-stressed parent and chick black-legged kittiwakes are shown (as black bars) for comparative purposes (data from Kitaysky et al. 1999a,b).

imental adult kittiwakes, we conducted regular surveys from 1 June to 1 July at the colony.

Effect of implantation and corticosterone analyses

In parallel to the experiment, we tested the effects of subcutaneous corticosterone implantation on birds captured elsewhere at the colony. We captured undisturbed birds and collected the initial baseline blood samples by puncturing the alar vein and collecting blood in heparinized microhematocrit 100- μ l tubes. After collecting the blood sample, blood flow was stopped by application of cotton. We banded captured birds with a unique combination of color bands, implanted them (as described above), and released adults at the colony and placed chicks back in their nests. Three days later, birds were recaptured and blood samples were collected (as described above). All blood samples were collected within 0–3 min after capture and were considered to reflect baseline levels of corticosterone (Kitaysky et al., 1999b).

After collecting blood, we emptied hematocrit tubes into 0.5-ml vials, which were stored on ice. Within 12 h, blood samples were centrifuged and plasma was collected. Plasma samples were frozen at -20°C and transported to the University of Washington for radioimmunoassay analyses. We measured corticosterone concentrations in duplicate for each plasma sample in one assay after extraction in dichloromethane. Before extraction, we added tritiated corticosterone (2000 cpm) to each plasma sample to control for a loss of corticosterone during extraction. Recovery values of the labeled steroid following extraction ranged from 80–90% and were used to adjust assayed concentrations of corticosterone. For a detailed description of the radioimmunoassay analysis, see Wingfield and Farnier (1975) and Wingfield et al. (1992).

Radioimmunoassay analysis revealed that in 15-day-old black-legged kittiwakes, a single 25-mm silastic tube filled with crystallized corticosterone approximately tripled the initial baseline levels of corticosterone (Figure 1). The heightened corticosterone levels were similar to the increase of baseline levels of corticosterone (assayed as described above) observed in kittiwake chicks that were reared in captivity under conditions of moderate food deprivation (Figure 1; Kitaysky et al., 1999a). In parent kittiwakes, the administered amount of crystallized corticosterone (two 25-mm implants) increased base-

line concentrations by about 10 ng/ml (Figure 1) and was expected to be metabolized within a 2- to 3-week period after implantation (Wingfield JC, personal observations). Thus, in this study the implantation elevated levels of corticosterone to a concentration and for a period similar to those observed in parent kittiwakes rearing their young during food shortages (Figure 1; Kitaysky et al., 1999b).

Statistical analyses

We considered each individual nest as an independent sample unit. Therefore, we calculated chick begging rates and food provisioning rates as mean values per each nest. Likewise, we calculated parameters of nest attendance by parents as mean values per each nest. Age of chick was not significantly different among the treatments and did not significantly affect any of the measured parameters of chick and parent behaviors, and therefore we excluded age from further statistical analyses. We compared begging rates among all four treatments using a two-way ANOVA (blocked by nest) with experimental treatment and brood size as factors (followed by LSD planned-comparison post-hoc test, which includes adjustments for multiple tests). We compared food provisioning rates among all four treatments using two-way ANOVA (blocked by nest) with experimental treatment and brood size as factors (followed by LSD planned-comparison post-hoc test). We compared proportions of time chicks were unattended by parents among all four treatments using median tests (blocked by nest) with experimental treatments as factor. We compared the behavioral characteristics of parents between nests with corticosterone-implanted and sham-implanted chicks using statistical tests for independent samples, where the experimental treatment (blocked by nest) was used as a grouping variable. We compared the behavioral characteristics of corticosterone-implanted and sham-implanted parents using statistical tests for independent samples. We examined the effects of the experimental treatments on the behavior of mates within a pair using paired-sample comparisons (paired by nest).

If data violated the assumptions for parametric tests (Sokal and Rohlf, 1981), we used nonparametric equivalents. We completed computation of statistical tests using STATISTICA.

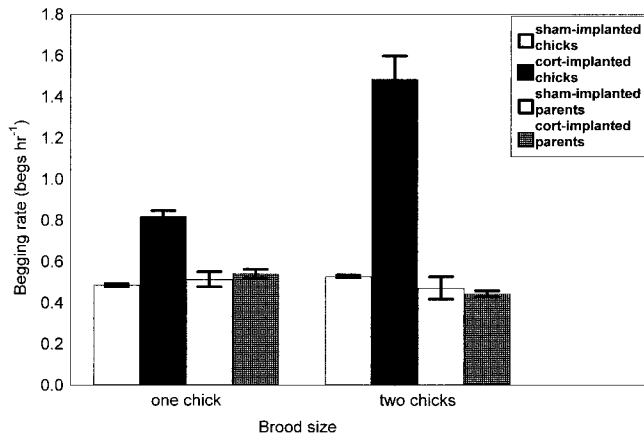


Figure 2
Behavioral responses of black-legged kittiwake chicks to experimentally increased circulating levels of corticosterone (means \pm SE; $n = 3$ nests per each treatment).

RESULTS

Chick's responses to experimental treatments

Begging rates

Experimental treatments had a significant effect on chick begging rates (two-way ANOVA, $F_{3,16} = 21.76$, $p < .001$; Figure 2). Corticosterone-implanted chicks begged more frequently than sham-implanted controls and more than chicks in the other two treatments (post-hoc test, $p < .001$ for all cases between the nests with corticosterone-implanted chicks and the nests either with sham-implanted chicks, corticosterone-implanted parents, or sham-implanted parents; Figure 2). Furthermore, there was a significant interaction between treatment and brood size ($F_{3,16} = 4.095$, $p = .025$); corticosterone-implanted chicks begged almost twice as much in broods of two than in broods of one (post-hoc test, $p < .001$; Figure 2). Brood size did not affect begging in the nests with sham-implanted chicks, corticosterone-implanted parents, or sham-implanted parents (post-hoc test, $p \geq .273$ for all cases; Figure 2).

Aggression

We did not observe a significant amount of aggression in the nests with two siblings. The only attacks of a smaller chick by its bigger sibling were observed in one of the nests with sham-implanted chicks.

Parent's responses to experimental treatments

Feeding rate

Experimental treatments had a significant effect on the feeding of chicks by the parents (two-way ANOVA, $F_{3,16} = 6.22$, $p = .005$; Figure 3). Corticosterone-implanted chicks were fed more frequently than sham-implanted chicks (post-hoc test, $p < .001$), than chicks at the nests with corticosterone-implanted parents (post-hoc test, $p = .028$), and than chicks at the nests with sham-implanted parents (post-hoc test, $p = .016$). Feeding rates were not significantly different between the nests with corticosterone-implanted and sham-implanted parents (post-hoc test, $p = .787$). Brood size did not affect feeding rate ($F_{1,16} = 0.74$, $p = .402$; Figure 3).

Nest attendance

Parents of corticosterone-implanted chicks made more trips (5.3 ± 0.95 [SE] trips per parent during a 2-day period, $n = 6$) away from the nest than did parents of sham-implanted

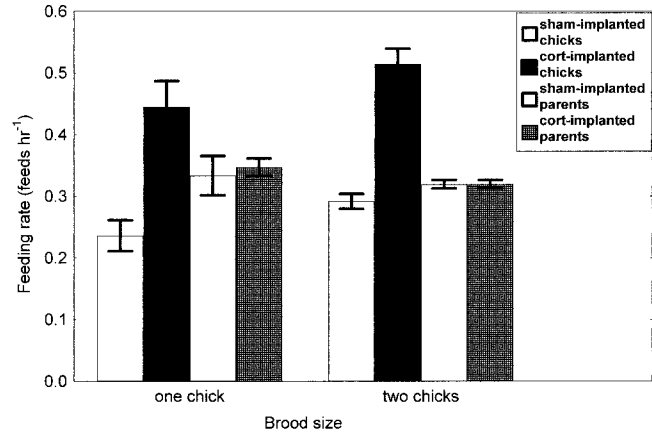


Figure 3
Behavioral responses of parent black-legged kittiwakes to experimentally increased circulating levels of corticosterone in their chicks (means \pm SE; $n = 3$ nests per each treatment).

chicks (3.5 ± 0.26 , $n = 6$; Kruskal-Wallis test, $H_1 = 6.23$, $n = 12$, $p = .013$). Corticosterone-implanted parents made more trips (4.5 ± 0.34 [SE] trips per 2-day period, $n = 6$) away from the nest than did sham-implanted parents (3.2 ± 0.41 , $n = 6$; ANOVA, $F_{1,10} = 12.31$, $p = .006$) and their untreated mates (3.0 ± 0.26 , $n = 6$; paired t test, $t = 6.71$, $df = 5$, $p = .001$).

Corticosterone-implanted parents spent less time (298.2 ± 27.24 [SE] min per 2-day period, $n = 6$) brooding/guarding chicks compared to sham-implanted parents (668.5 ± 76.85 , $n = 6$; Kruskal-Wallis test, $H_1 = 8.31$, $n = 12$, $p = .004$). Corticosterone-implanted parents also spent significantly less time brooding/guarding chicks compared to their untreated mates (760.0 ± 106.55 , $n = 6$; Wilcoxon matched pairs test, $Z = 1.199$, $n = 6$, $p < .05$). Sham-implanted parents spent a similar amount of time brooding/guarding chicks as their untreated mates (617.33 ± 78.95 , $n = 6$; paired t test, $t = .329$, $df = 5$, $p = .756$).

Chicks of corticosterone-implanted parents spent more time unattended by either of the parents compared to chicks in all other treatments (Figure 4; median test: $\chi^2 = 9.33$, $df = 3$, $p = .025$).

Chick provisioning rates by corticosterone-implanted parents

The experimental increase in corticosterone levels did not alter chick provisioning rates of corticosterone-implanted parents, which fed their chicks at rates (0.174 ± 0.012 [SE] feeds/h, $n = 6$) similar to those of sham-implanted parents (0.167 ± 0.015 , $n = 6$; ANOVA, $F_{1,10} = 0.122$, $p = .734$). Feeding rates were also similar between implanted and untreated mates within a pair (paired t test, $t = 0.349$, $df = 5$, $p = .741$, and $t = 0.466$, $df = 5$, $p = .661$, for nests with sham-implanted and corticosterone-implanted parents, respectively).

Survival and resighting of experimental birds

All experimental and control chicks survived until fledging. All experimental and control parents survived during a 3-week period after the implantation and reared their chicks successfully until fledging. During the reproductive season of 1998, five out of six corticosterone-implanted parents failed to return to the nesting colony, whereas all other parents (except one of the sham-implanted birds) returned to the colony. During the reproductive season of 1999, the individuals that were missing in 1998 were also not resighted at the colony, whereas all other birds returned to the colony. The proportion of cor-

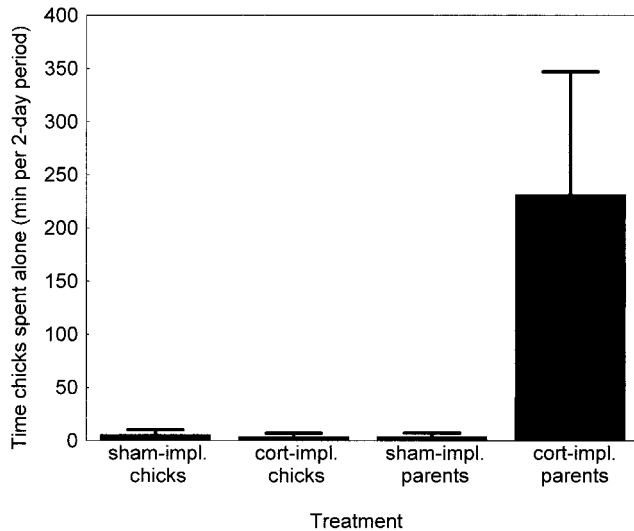


Figure 4
Time spent by black-legged kittiwake chicks unattended by parents (means \pm SE; $n = 6$ nests per each treatment).

corticosterone-implanted parents that failed to return to the breeding colony was significantly larger than in sham-implanted parents (Fisher's Exact test, $p = .04$).

DISCUSSION

Behavioral responses to the experimental increased levels of corticosterone in chicks

Experimental studies have shown that hunger in the nest-bound chick results in increased begging (e.g., Bengtsson and Ryden, 1983; Cotton et al., 1996; Henderson, 1975). Furthermore, recent empirical studies showed that blue-footed booby (*Sula nebouxi*) chicks release corticosterone in response to short-term food deprivation (Nunez-de la Mora et al., 1996), as do food-restricted black-legged kittiwake chicks (Kitaysky et al., 1999a). In the present study, we have taken these observations a step further to show that high corticosterone levels increase chick begging rates and increase rates of food provisioning by parents.

Our study suggests that begging behavior is regulated through secretion of corticosterone. Corticosterone secretion likely maintains and restores animal homeostasis in response to environmental changes (e.g., Silverin, 1998). Our study shows clearly that the release of corticosterone in hungry kittiwake chicks allows them to restore depleted energy reserves by modifying the behavior of their parents. However, such regulation is not without costs. Chronic elevation of corticosterone is known to suppress memory and immune systems, promote wasting of muscle tissue, and cause neuronal cell death (Sapolsky, 1992; Sapolsky et al., 1986). Thus, the regulation of begging through secretion of corticosterone is likely to be associated with benefits and costs, which must be balanced by a begging chick.

The regulation of begging through secretion of corticosterone might represent an evolutionarily stable signaling system as a resolution of parent-offspring conflict in birds. Our study suggests that parent kittiwakes probably assess the physiological condition of their chicks by monitoring begging. In such a system, a chick can misrepresent its requirements to acquire more food than it needs (Godfray, 1995b). Cheating may be prevented if there is a cost associated with begging that is larger than the benefits of the extra food obtained by a cheat-

ing chick (Godfray, 1995b). If continuous begging is associated with a prolonged secretion of corticosterone, then a cheating chick would suffer detrimental effects of chronically elevated levels of corticosterone. Thus, if cheating is associated with high levels of corticosterone, exaggerated begging might be costly, and a cheating chick may endanger its future survival. Our conclusion hinges on the assumption that continuous begging requires continuous secretion of corticosterone, which remains to be shown. Clearly, future studies addressing hormonal regulation of begging and potential long-term effects of chronic elevation of corticosterone levels in nest-dependent chicks are needed.

In addition to effects of corticosterone, interactions between chicks within a brood probably increase chick begging rates. In particular, we found that corticosterone-implanted chicks in broods of two begged more frequently than singletons. In contrast, we did not record any aggression between siblings in the nests with corticosterone-implanted chicks. This supports earlier observations that competition for food between food-stressed siblings is initially expressed by increased begging (Muller and Smith, 1978; Smith and Montgomerie, 1991). In the black-legged kittiwake, Braun and Hunt (1983) observed higher begging rates of hungry chicks when they occurred in broods of two compared to singletons. Similar observations were reported for some species of birds (e.g., Harper, 1986; for cotingas, Cotingidae), but in other species (Cotton et al., 1996; Kacelnik et al., 1995; for European starling, *Sturnis vulgaris*) a chick tends to beg in relation to its own condition regardless of the behavior of its nest mates. It is not known yet how important phylogenetic constraints are in determining chick begging strategies, and differences among different studies might reflect that phenomenon. Nevertheless, our observations are consistent with the theoretical prediction that the begging rate of a chick depends on its own condition and on conditions of its nest mates (Godfray, 1995a). Thus, although high levels of corticosterone increase begging in black-legged kittiwake chicks, further escalation of a chick's begging probably depends on the begging levels of its sibling.

Although corticosterone-implanted chicks in broods of two begged at almost twice the rate of singletons, parents did not feed them at twice the rate of corticosterone-implanted singletons (mean feeding rates differed by 13% between chicks in broods of two and singletons). In contrast to these results, other experimental studies have shown that parental provisioning is proportional to chick begging (e.g., Kacelnik et al., 1995). However, parental ability to increase feeding rates is likely to be limited, and it is possible that parents of all corticosterone-implanted chicks were probably provisioning food at or near maximal rates. On the other hand, we cannot exclude the possibility that somehow parent kittiwakes are able to discriminate between changes in a chick's begging behavior due to the change in its physiological condition from changes reflecting social interactions between siblings within a brood.

Foraging conditions were favorable for kittiwakes breeding in the study area in 1997 (Kitaysky et al., 1999b; Piatt JF, unpublished data). Thus, we observed parental responses to the corticosterone-induced begging of chicks in a situation when parents could provide more food. Responses of parent kittiwakes to chick demands might differ under less favorable foraging conditions, thereby changing provisioning rates. If parents cannot provide food in response to chick demands, then aggression leading to siblicide would probably occur (Braun and Hunt, 1983). Before reaching this point, however, begging behavior would offer some evolutionary advantages over aggressive behavior. Begging behavior probably requires less energy (McCarty, 1996; Soler et al., 1999) and entails less risk of injury than aggressive behavior.

Behavioral responses to the experimental increased levels of corticosterone in parents

This study also suggests a physiological mechanism for the regulation of resource allocation by adult black-legged kittiwakes during chick rearing. We found that corticosterone-implanted parent kittiwakes performed more trips away from the nests than did sham-implanted parents. We assumed when birds were away from the nests, they were foraging. This assumption seems to be reasonable (e.g., Monaghan et al., 1996) and was justified by direct observations of chick-rearing black-legged kittiwakes (Irons, 1998). Kitaysky et al. (1999b) have shown that parent kittiwakes respond to food shortages by increased secretion of corticosterone. Moderate increases in corticosterone secretion are known to increase foraging activities (Astheimer et al., 1992; Wingfield et al., 1998) and food intake (Wingfield and Ramenofsky, 1999). Thus, we suggest that frequent trips of the corticosterone-implanted parent kittiwakes away from the nests were probably due to an increase in their food demands.

Our results show that in response to the experimental increase in circulating levels of corticosterone, adult kittiwakes increased foraging at the expense of guarding their chicks. This resulted in a considerable increase in the amount of time that chicks were unattended and potentially vulnerable to predation. A similar increase in the time that young kittiwake chicks spent unattended during poor foraging conditions was observed by Roberts and Hatch (1993). High corticosterone levels also affect parental behavior in other species (Silverin, 1986; Wingfield et al., 1997, 1998). In contrast to other studies of the experimentally increased corticosterone levels in chick-rearing birds (e.g., Silverin, 1986), our results do not demonstrate an effect of high corticosterone on the breeding success of black-legged kittiwakes. Yet we examined the relationship between high corticosterone and parental behavior in the context of a food-rich colony where nonexperimental parents were not off foraging as much, thereby protecting both their own chicks and the implanted birds' chicks from predators. However, food shortages are likely to affect the behavior of all birds breeding at a particular colony in a similar manner, and all affected birds would be leaving their chicks unattended. In this manner, increased corticosterone secretion can be an important factor determining breeding success of black-legged kittiwakes during food shortages.

The major prediction of life-history theory is that long-lived birds should balance survival of their current offspring with their own survival (Linden and Møller, 1989). Current reproductive effort affects residual reproductive value in the black-legged kittiwake (Golet et al., 1998; Hatch et al., 1993, 1994). Kitaysky et al. (2000) have shown that a decrease in food abundance causes an increase in energy expenditures of parent kittiwakes, whereas growth rates of their chicks are not affected. An increase in parental effort of black-legged kittiwakes results in a decrease of their body condition (through a depletion of fat reserves), which may affect their postreproductive survival (Golet and Irons, 1999). A depletion of fat reserves in parent kittiwakes results in elevation of circulating levels of corticosterone (Kitaysky et al., 1999b), which might affect their return rate to the breeding colony (this study). In this study we established that the individuals with experimentally elevated levels of corticosterone increased foraging at the expense of brooding/guarding their chicks, but did not alter their chick provisioning rates and could suffer a long-term effect of chronically elevated levels of corticosterone.

We thank Roman Kitaysky, Stephani Zador, Mike Shultz, and April Nielsen for their help during the experiment. We thank David Westneat, Marc Mangel, Morgan Benowitz-Frederiks, Samrrah Raouf, Ig-

nacio Moore, and anonymous reviewers for reading the manuscript and for providing numerous useful comments. Financial support for this study was provided through EVOS Trustee Council (Restoration Projects 98163M and 99479) to J.F.P. and A.S.K., and National Science Foundation grant OPP9530826 to J.C.W. The Soldovia Native Corporation granted permissions to work on Gull Island. The experimental manipulations with birds conformed to the rules of Laboratory Animal Care and Use Protocol, University of Washington.

REFERENCES

- Astheimer, L.B., Buttemer WA, Wingfield JC, 1992. Interactions of corticosterone with feeding, activity and metabolism in passerine birds. *Ornis Scand* 23:355–365.
- Bengtsson H, Ryden O, 1983. Parental feeding rate in relation to begging behavior in asynchronously hatched broods of the great tit *Parus major*. *Behav Ecol Sociobiol* 12:243–251.
- Braun BM, Hunt GL, 1983. Brood reduction in black-legged kittiwakes. *Auk* 100:469–476.
- Bray MM, 1993. Effect of ACTH and glucocorticoids on lipid metabolism in the Japanese quail, *Coturnix coturnix japonica*. *Comp Physiol Biochem A* 105:689–696.
- Chaurand T, Weimerskirch H, 1994. The regular alternation of short and long trips in the blue petrel *Halobaena caerulea*: a previously undescribed strategy of food provisioning in a pelagic seabird. *J Anim Ecol* 63:275–282.
- Cherel Y, Robin J-P, Le Maho Y, 1988. Physiology and biochemistry of long-term fasting in birds. *Can J Zool* 66:159–166.
- Cody ML, 1966. A general theory of clutch size. *Evolution* 20:174–184.
- Cotton PA, Kacelnik A, Wright J, 1996. Chick begging as a signal: are nestlings honest? *Behav Ecol* 7:178–182.
- Cotton PA, Wright J, Kacelnik A, 1999. Chick begging strategies in relation to brood hierarchies and hatching asynchrony. *Am Nat* 153:412–420.
- Coulson JC, Wooler RD, 1984. Incubation under natural conditions in the kittiwake gull, *Rissa tridactyla*. *Anim Behav* 32:1204–1215.
- Drent RH, Daan S, 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225–252.
- Godfray HCJ, 1991. Signaling of need by offspring to their parents. *Nature* 352:328–330.
- Godfray HCJ, 1995a. Evolutionary theory of parent-offspring conflict. *Nature* 376:133–138.
- Godfray HCJ, 1995b. Signaling of need between parents and young: parent-offspring conflict and sibling rivalry. *Am Nat* 146:1–24.
- Golet GH, Irons DB, 1999. Raising young reduces body condition and fat stores in black-legged kittiwakes. *Oecologia* 120:530–538.
- Golet GH, Irons DB, Estes JA, 1998. Survival costs of chick rearing in black-legged kittiwakes. *J Anim Ecol* 67:827–841.
- Harper AB, 1986. The evolution of begging: sibling competition and parent-offspring conflict. *Am Nat* 128:99–114.
- Hatch SA, Kondratyev AY, Kondratyeva LF, 1994. Comparative demography of black-legged kittiwakes (*Rissa tridactyla*) in the Gulf of Alaska and Sea of Okhotsk. Bridges of the Sciences between North America and the Russian Far East. 45th Arctic Science Conference. Abstracts, book 1. Russian Academy of Sciences and American Association for the Advancement of Science. Vladivostok: Dalnauka.
- Hatch SA, Roberts BD, Fadley BS, 1993. Adult survival of black-legged kittiwakes *Rissa tridactyla* in a Pacific colony. *Ibis* 135:247–254.
- Henderson BA, 1975. Role of the chick's begging behavior in the regulation of parental feeding behavior of *Larus glaucescens*. *Condor* 77:488–492.
- Iacovides S, Evans RM, 1998. Begging as graded signals of need for young in young ring-billed gulls. *Anim Behav* 56:79–85.
- Irons DB, 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology* 79:647–655.
- Kacelnik A, Cotton PA, Stirling L, Wright J, 1995. Food allocation among nestling starlings: sibling competition and the scope of parental choice. *Proc R Soc Lond B* 259:259–263.
- Kilner R, 1995. When do canary parents respond to nestling signals of need? *Proc R Soc Lond B* 269:343–348.
- Kitaysky AS, Hunt GL, Flint EN, Rubega MA, Decker MB, 2000. Resource allocation in breeding seabirds: responses to fluctuations in their food supply. *Mar Ecol Prog Ser* 206:283–296.

- Kitaysky AS, Piatt JF, Wingfield JC, Romano M, 1999a. Stress response of black-legged kittiwake chicks in relation to dietary restrictions. *J Comp Physiol B* 169:303–310.
- Kitaysky AS, Wingfield JC, Piatt JF, 1999b. Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. *Funct Ecol* 13:577–584.
- Leonard ML, Horn AG, 1996. Provisioning rules in tree swallows. *Behav Ecol Sociobiol* 42:431–436.
- Linden M, Møller AP, 1989. Cost of reproduction and covariation of life history traits in birds. *Trends Ecol Evol* 4:367–371.
- McCarty JP, 1996. The energetic cost of begging in nestling passerines. *Auk* 113:178–188.
- Monaghan P, Wright PJ, Bailey MC, Uttley JD, Walton P, Burns MD, 1996. The influence of changes in food abundance on diving and surface-feeding seabirds. In: *Studies of high-latitude seabirds*. 4. Trophic relationships and energetics of endotherms in cold ocean systems. *Occas Papers Can Wildl Serv* 91:10–19.
- Muller RE, Smith DG, 1978. Parent-offspring interactions in zebra finches. *Auk* 95:485–495.
- Nunez-de la Mora A, Drummond H, Wingfield JC, 1996. Hormonal correlates of dominance and starvation-induced aggression in chicks of the blue-footed booby. *Ethology* 102:748–761.
- Price K, Ydenberg R, 1995. Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. *Behav Ecol Sociobiol* 37:201–208.
- Ricklefs RE, Schew WA, 1994. Foraging stochasticity and lipid accumulation by nestling petrels. *Funct Ecol* 8:159–170.
- Roberts BD, Hatch SA, 1993. Behavioral ecology of black-legged kittiwakes during chick rearing in a falling colony. *Condor* 95:330–342.
- Sapolsky RM, 1992. Neuroendocrinology of the stress-response. In: *Behavioral endocrinology* (Becker JB, Breedlove SM, Crews D, eds). Boston, Massachusetts: MIT Press; 287–324.
- Sapolsky RM, Krey LC, McEwen BS, 1986. The neuroendocrinology of stress and aging: the glucocorticosteroid cascade hypothesis. *Endocr Rev* 7:284–301.
- Silverin B, 1986. Corticosterone binding proteins and behavioral effects of high plasma levels of corticosterone during the breeding period in the pied flycatcher. *Gen Comp Endocrinol* 64:67–74.
- Silverin B, 1998. Behavioural and hormonal responses of the pied flycatcher to environmental stresses. *Anim Behav* 55:1411–1420.
- Smith HG, Montgomerie R, 1991. Nestling American robins compete with siblings by begging. *Behav Ecol Sociobiol* 29:397–312.
- Sokal RR, Rohlf FJ, 1981. *Biometry*, 2nd ed. San Francisco: W.H. Freeman.
- Soler M, Soler JJ, Martinez JG, Moreno J, 1999. Begging behaviour and its energetic cost in great spotted cuckoo and magpie host chicks. *Can J Zool* 77:1794–1800.
- Stamps J, 1993. Begging in birds. *Ethology* 3:69–77.
- Trivers RL, 1974. Parent-offspring conflict. *Am Zool* 14:249–264.
- Veiga JAS, Roselino ES, Migliorini RH, 1978. Fasting, adrenalectomy, and gluconeogenesis in the chicken and a carnivorous bird. *Am J Physiol* 234:R115–R121.
- Weimerskirch H, Chastel O, Chaurand T, Ackerman L, Hindermeier X, Judas J, 1994. Alternate long and short foraging trips in pelagic seabird parent. *Anim Behav* 47:472–476.
- Wingfield JC, Bruener C, Jacobs J, 1997. Corticosterone and behavioral responses to unpredictable events. In: *Perspectives in avian endocrinology* (Harvey S, Etches RJ, eds). Bristol, UK: Journal of Endocrinology Ltd; 267–278.
- Wingfield JC, Farner DS, 1975. The determination of five steroids in avian plasma by radioimmunoassay and competitive protein binding. *Steroids* 26:311–327.
- Wingfield JC, Maney DL, Breuner CW, Jacobs JD, Lynn S, Ramenofsky M, Richardson RD, 1998. Ecological bases of hormone-behavior interactions: the “emergency life history stage.” *Am Zool* 38:191–206.
- Wingfield JC, Ramenofsky M, 1999. Hormones and behavioral ecology of stress. In: *Stress physiology in animals* (Balm PHM, ed). Sheffield, UK: Sheffield Academic Press; 1–51.
- Wingfield JC, Silverin B, 1986. Effects of corticosterone on territorial behavior of free-living male song sparrows, *Melospiza melodia*. *Horm Behav* 20:405–417.
- Wingfield JC, Vleck CM, Moore MC, 1992. Seasonal changes of the adrenocortical response to stress in birds of Sonoran Desert. *J Exp Zool* 264:419–428.
- Zahavi A, 1987. The theory of signal selection and some of its implications. In: *Proceedings of the International Symposium on Biological Evolution*. Bari, Italy: Adriatica Edetricia; 305–325.