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Recommended Citation

Henson, Shandelle M.; Weldon, Lynelle M.; Hayward, James L.; Greene, Daniel; Megna, Libby C.; and Serem, Maureen C., "Coping Behaviour as an Adaptation to Stress: Post-Disturbance Preening in Colonial Seabirds" (2012). *Faculty Publications*. 1532.

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Coping behaviour as an adaptation to stress: post-disturbance preening in colonial seabirds

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(Received 22 November 2010; final version received 13 July 2011)

In humans, coping behaviour is an action taken to soothe oneself during or after a stressful or threatening situation. Some human behaviours with physiological functions also serve as coping behaviours, for example, comfort sucking in infants and comfort eating in adults. In birds, the behaviour of preening, which has important physiological functions, has been postulated to soothe individuals after stressful situations. We combine two existing modelling approaches – logistic regression and Darwinian dynamics – to explore theoretically how a behaviour with crucial physiological function might evolve into a coping behaviour. We apply the method to preening in colonial seabirds to investigate whether and how preening might be co-opted as a coping behaviour in the presence of predators. We conduct an in-depth study of the environmental correlates of preening in a large gull colony in Washington, USA, and we perform an independent field test for comfort preening by computing the change in frequency of preening in gulls that were alerted to a predator, but did not flee.

Keywords: animal behaviour; Darwinian dynamics; coping behaviour; glaucous-winged gull; preening

AMS Subject Classification Code: 92D15; 92D25; 92D40; 92D50

1. Introduction

In this paper, we present a mathematical framework for modelling the microevolution of animal behaviour. In particular, we consider how a behaviour with physiological function might evolve into a coping behaviour that can soothe an animal during times of stress. We apply the modelling methodology to gulls, a classic animal model in behavioural studies, and consider whether preening might be adapted as a coping behaviour in response to increasing disturbances due to rebounding eagle populations.

The study has four goals. The first goal is to combine the techniques of logistic regression and Darwinian dynamics to develop a general model for the microevolution of animal behaviour that can describe the evolution of coping behaviour. The second goal is to conduct an in-depth study

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of the environmental correlates of preening at a large gull colony in Washington, USA. The third goal is to construct a specific model of the evolution of comfort preening in gulls in the presence of eagle disturbances. The fourth goal is to conduct an independent empirical test of the existence of comfort preening in the gull colony post-eagle disturbance. Each of these topics deserves a brief introduction.

1.1. *Hypothesis of coping behaviour as an evolutionary adaptation to stress*

The first goal of this study is to develop a mathematical model for the evolution by natural selection of animal behaviour that can describe the evolution of a coping behaviour. In humans, a coping behaviour is ‘a characteristic and often automatic action or set of actions taken in dealing with stressful or threatening situations’ [43] in an attempt to reduce stress and minimize personal or interpersonal conflict [40,45,47]. ‘Comfort eating’, for example, can serve as a coping behaviour in humans [15], and ‘comfort sucking’ can pacify an infant [1]. In birds, the behaviour of preening, shown to be important for maintenance of flight feathers, thermoregulation, and parasite removal [12,39], has been postulated to serve as a coping behaviour that soothes birds after a stressful situation [16,27,30]. In what follows, we refer to this hypothetical type of preening as ‘comfort preening’.

Given that the emotional state of non-human animals cannot be measured directly, it is not possible to provide conclusive evidence that they engage in self-soothing coping behaviours. It is possible, however, to measure physiological responses to stressors; and one could measure in the laboratory how such responses are modified by behaviours that appear analogous to human coping behaviours. A less conclusive, but nevertheless suggestive, field approach is to measure the incidence of the hypothetical coping behaviour before and after a point disturbance (a stressor of short duration) in a large number of animals. We use this latter approach.

Many behaviours are heritable phenotypic traits shaped by natural selection [20]. Co-option is the process of natural selection by which an extant trait comes to be utilized for a new purpose [3]. In particular, an extant behaviour with direct physiological function (such as eating in humans or preening in birds) might be co-opted as a coping behaviour. Although some of the effects of behaviours such as eating and preening upon fitness are obvious, the selective advantages of using these behaviours for comfort in times of stress are less clear. In colonial birds, for example, comfort preening may be advantageous if it decreases territorial disputes after disturbances, but may also be deleterious to fitness if it decreases alertness to predators. Our goal is to construct a model that can describe the evolutionary outcome of these trade-offs.

Darwin’s postulates – that the tendency for populations to grow exponentially leads to competition for limited resources, that phenotypic traits affect the outcome of competition, and that phenotypic traits are heritable – are elegant and well tested in both field and laboratory [19]. The genetic basis, however, for a given heritable trait – and perhaps especially for a behavioural trait – often is difficult to evaluate.

In this study, we use the technique of Darwinian dynamics [44], which models the microevolutionary change by tracking mean phenotypic traits in the dynamic population rather than by tracking gene frequencies.

1.2. *Environmental correlates of preening in glaucous-winged gulls*

The second goal of this study is to analyse the environmental correlates of preening behaviour in a large colony of glaucous-winged gulls (*Larus glaucescens*) on Protection Island, Washington. Due to their large size, visibility, colonial breeding, and rich array of behaviours, gulls have served as classic animal models in behavioural studies [41].

Preening is the behaviour in which a sitting or standing bird pulls feathers through its bill and/or moves its head in a smoothing motion over the body [31]. Preening occupies up to 23% of the time of first-year mourning doves [29] and 27% of glaucous-winged gulls' waking time on their territory [30]. Ornithologists and ethologists have identified a variety of contexts within which preening occurs and have postulated a variety of functions for this activity. Gulls preen after flight [17], and the incidence of preening in herring gulls (*Larus argentatus*) and terns (*Thalasseus sandvicensis* and *Sterna hirundo*) increases after their feathers have become damp or water-soaked [27,36,37]. In day-old domestic poultry, preening is associated with increases in sound intensity and photointensity and decreases in temperature [4]. Preening increases in response to increased egg temperature in brooding ringed turtle doves (*Streptopelia risoria* [18]), and increasing relative humidity increases the incidence of preening among glaucous-winged gulls [24].

In this study, we use a logistic regression model to quantify the response of preening to humidity, temperature, solar elevation, wind speed, tide height, barometric pressure, and stage of breeding season.

1.3. Preening as a hypothetical coping behaviour after eagle disturbance

The third goal of this study is to apply the Darwinian dynamics model to glaucous-winged gulls and explore the hypothesis that preening may serve as a coping behaviour that soothes birds after periods of disturbance.

The disturbances in our application are bald eagle (*Haliaeetus leucocephalus*) flyovers of the colony. Eagles predate eggs, chicks, and adult seabirds. Frequent eagle flyovers of seabird colonies – whether or not the flyovers lead to predatory events – produce stress in birds attending the colonies [23,33,46]. During the decades in which eagle numbers were low due to the effects of DDT, North American seabird colonies on islands isolated from ground predators experienced little predation of any type. Eagle populations have rebounded dramatically, however, in the past three decades, resulting in relatively sudden and dramatic increases in the rate of colony disturbance [21,23,33,46].

Past studies have associated preening not only with environmental factors, but also with psychological factors. Early ethologists identified some instances of preening as a form of 'displacement', a behaviour occurring during conflict situations and which 'appears to be irrelevant to any of the tendencies in conflict' [25]. For example, European starlings (*Sturnus vulgaris*) may preen vigorously during a fight with other starlings [42], and chaffinches (*Fringilla coelebs*) preen when the tendency to approach and to fly away have been interpreted to be in equilibrium [38]. Furthermore, commensurate with our hypothesis, preening in gulls and terns has been postulated to soothe or quiet these birds after extended periods of disturbance [16,27,30].

Despite its frequent occurrence, preening does incur costs. For example, Redpath [34] observed that dunlin (*Calidris alpina*) experience obscured vision during preening because during this activity feathers cover the eyes thus increasing the risk of predation. Moreover, the energy cost for preening is approximately twice the basal metabolic rate [14,22]. Gains, however, include cleaning, straightening, and repairing feathers for better flight and thermoregulation [39], reduction of ectoparasite load [8,10,13] with an increase in mating success [7], and even social communication [5,32].

In applying the model of coping behaviour to preening, we hypothesize that the extant behaviour of preening, which has direct physiological function as quantified by a logistic regression model, potentially could be co-opted as a coping behaviour given the increased level of eagle activity. For this to occur, any losses in fitness attributable to preening must be offset by significant gains [30].

1.4. Empirical evidence for comfort preening

The fourth goal of this study is to measure directly the presence of comfort preening on the Protection Island colony. We accomplish this by comparing the incidence of preening before and after the occurrence of specific types of bald eagle flyovers.

2. Model

In this section, we construct a model in two stages. First, we give a general framework for modelling the microevolution of a behaviour in a dynamic population; we denote the focal behaviour as ‘behaviour B ’. Second, we construct a specific model for the application to preening as a coping behaviour in gulls.

2.1. General framework

We construct a general framework in three stages. First, we present a logistic regression model for behaviour B and assume that the coefficients are subject to natural selection. Second, we pose a population model with logistic growth whose parameters depend on the behaviour coefficients. (Note that the use of logistic regression is unrelated to the assumption of logistic population growth.) Third, we formulate the Darwinian dynamics model that couples the population model with dynamic equations for the evolving coefficients.

We begin with a logistic regression model for a behaviour B that occurs in response to various biotic and abiotic cues. Logistic regression [26] is a technique commonly used to quantify the effect of factors on a binary variable (the behaviour occurs, or it does not occur). In this approach the ‘log odds’ of the occurrence of behaviour B is regressed on a vector $\mathbf{x} = (x_1, x_2, \dots, x_n)$ of factors

$$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \sum_{j=1}^n \beta_j x_j, \quad (1)$$

where p is the probability of behaviour B . The intercept β_0 calibrates the baseline occurrence of behaviour B when all factors are zero, and the regression coefficients $\boldsymbol{\beta} = (\beta_1, \dots, \beta_n)$ quantify the response of behaviour B to changes in the factors. The right-hand side of Equation (1) also can include ‘interaction terms’ of the form $\beta_{ij}x_i x_j$.

The coefficients $\boldsymbol{\beta}$ have a convenient interpretation. For non-interaction terms, if factor x_i increases by c units while all other factors remain constant, then the log odds changes by $\beta_i c$ units:

$$\ln\left(\frac{p_2}{1-p_2}\right) - \ln\left(\frac{p_1}{1-p_1}\right) = \left(\beta_0 + \beta_i(x_i + c) + \sum_{\substack{j=1 \\ j \neq i}}^n \beta_j x_j\right) - \left(\beta_0 + \sum_{j=1}^n \beta_j x_j\right) = \beta_i c, \quad (2)$$

where p_1 and p_2 are the probabilities of preening before and after the change, respectively. Thus, the ‘odds ratio’ is

$$\frac{p_2/(1-p_2)}{p_1/(1-p_1)} = e^{\beta_i c}. \quad (3)$$

This means that, given an increase in factor x_i by c units, the odds of behaviour B are $e^{\beta_i c}$ times what they were before. (For interaction terms, the computation is similar but slightly more complicated.) Thus, if $\beta_i > 0$ ($\beta_i < 0$), then the odds ratio is greater (less) than one, and so the odds of behaviour

B have increased (decreased). In this study, we assume that the regression coefficients β are subject to natural selection.

We now pose a population model, the parameters of which depend on the regression coefficients β . For simplicity of illustration, we assume population growth is logistic and can be modelled as

$$\frac{dN}{dt} = b(\beta)N - d(\beta)N^2. \quad (4)$$

Here $b(\beta)$ is the net per capita rate of change at small population sizes, that is, the balance of mean birth and death rates for individuals having traits β in the absence of crowding. Also, $d(\beta)N$ represents the density-dependent per capita death rate due to crowding effects for individuals having traits β .

Finally, we incorporate the population model into a Darwinian dynamics model that tracks microevolutionary changes in mean heritable traits β on the timescale of the population dynamics [44]. In this case, the Darwinian dynamics model is the $(n + 1)$ -dimensional system

$$\begin{aligned} \frac{dN}{dt} &= b(\beta)N - d(\beta)N^2, \\ \frac{d\beta_i}{dt} &= s_i^2 \frac{\partial G}{\partial \beta_i} + \sum_{j \neq i} \delta_{ij}^2 \frac{\partial G}{\partial \beta_j}, \quad i = 1, 2, \dots, n, \end{aligned} \quad (5)$$

where the ‘fitness generating function’ G is defined as the per capita growth rate $(1/N)dN/dt$ [44]. Each s_i is a positive constant called the ‘speed of evolution’ for coefficient β_i , coefficient s_i^2 is the variance of trait β_i in the population, and coefficient δ_{ij}^2 is the covariance of traits β_i and β_j [44, p. 138].

2.2. A model for comfort preening in gulls

In this section, we propose a specific form of Equation (5) for our particular application. We proceed under the general assumptions that (1) comfort preening is co-opted from preening behaviour with a direct physiological function; (2) comfort preening redirects energy from other functions and thus can be deleterious to physiological health; (3) comfort preening can lead to mortality due to lack of alertness during stressful situations such as eagle flyovers, and (4) comfort preening can decrease density-dependent mortality, for example, by soothing inter-individual conflict during or immediately after stressful situations.

In particular, we assume that the first $n - 1$ regression coefficients $\beta_1, \beta_2, \dots, \beta_{n-1}$ quantify the response of preening to $n - 1$ environmental factors, and that coefficient β_n quantifies the response of preening to stress (eagle disturbance in our application). We further assume that the vital rate $b(\beta)$ in Equation (4) can be expressed as

$$b(\beta) = a(\beta) - c(\beta), \quad (6)$$

where $a(\beta)$ is the net per capita rate of change (the balance of birth and death rates) at small population sizes in the absence of predation, and $c(\beta)$ represents an additional death rate (at small population sizes) due to predation. In our application, $a(\beta)$ is a measure of the general physiological health of an individual possessing traits β , and $c(\beta)$ is a measure of the vulnerability to predation of an individual possessing traits β .

We assume that, in the absence of stress, deviation of the coefficients $\beta_1, \beta_2, \dots, \beta_{n-1}$ from optimal values $\alpha_1, \alpha_2, \dots, \alpha_{n-1}$ results in a decrease in general physiological health. We also assume

that any change in preening behaviour as a response to stress decreases general physiological health. In particular, we assume

$$a(\boldsymbol{\beta}) = a_0 \exp\left(-\frac{1}{2} \sum_{j=1}^{n-1} \left(\frac{\beta_j - \alpha_j}{\sigma_j}\right)^2\right) \exp\left(-\frac{1}{2} \left(\frac{\beta_n}{\sigma_n}\right)^2\right) \quad (7)$$

for $a_0 > 0$, where $\beta_n > 0$ ($\beta_n < 0$) indicates an increase (decrease) in preening behaviour in the presence of stress. General physiological health $a(\boldsymbol{\beta})$ is optimal (with value a_0), if and only if $\beta_i = \alpha_i$ ($i = 1, 2, \dots, n-1$) and $\beta_n = 0$.

We assume that an increase in preening in response to eagle disturbance ($\beta_n > 0$) may cause a gull to be less alert to predation. That is, the use of preening as a coping behaviour immediately after an eagle disturbance may lead to reduced alertness and hence higher mortality, given that departing eagles sometimes suddenly change course and quickly stoop into the colony. We also assume that a decrease in preening behaviour in response to disturbance ($\beta_n < 0$) may lead to more alertness and lower mortality. In particular, we assume $c(\boldsymbol{\beta})$ is a monotonically increasing function of β_n with values on the interval $(0, c_0)$ for $c_0 > 0$:

$$\begin{aligned} c(\boldsymbol{\beta}) &= c_0 h(\beta_n), \\ h &\in C^1(\mathbf{R}, (0, 1)), \\ h'(x) &> 0 \quad \forall x \in \mathbf{R}, \\ \lim_{x \rightarrow -\infty} h(x) &= 0 \quad \text{and} \quad \lim_{x \rightarrow \infty} h(x) = 1. \end{aligned} \quad (8)$$

An example of a function h satisfying these properties is $h(x) = 1/2 + (1/\pi) \arctan(\alpha_h x)$.

Finally, we assume that the coefficient $d(\boldsymbol{\beta})$ on the density-dependent death rate in Equation (4) can be decomposed into three components that we designate ‘environmental effects’ (due to environmental resource limitation caused by crowding), ‘psychological effects’ (due to inter-individual aggression that is reduced by coping behaviour), and ‘physiological effects’ (due to compromised physical health). We assume the component due to ‘environmental effects’ is constant $d_0 > 0$ and is unaffected by preening. We assume the component due to ‘psychological effects’ is a monotonically decreasing function of β_n with values on the interval $(0, d_1)$, for $d_1 > 0$. In our application, ‘psychological effects’ would include territory disputes (some of which are disabling or fatal), and cannibalism of chicks that are flushed into neighbouring territories during disturbances. An individual that engages in comfort preening post-disturbance might experience reduced mortality due to these factors, whereas an individual that preens less in response to disturbance might experience increased mortality. We assume the component due to ‘physiological effects’ increases when general physiological health $a(\boldsymbol{\beta})$ decreases. In our application, preening at rates greater than or less than those optimal for general physiological health might place a compromised bird at risk in a territorial dispute. In particular, we assume

$$d(\boldsymbol{\beta}) = d_0 + d_1 f(\beta_n) + d_2 \left(1 - \frac{a(\boldsymbol{\beta})}{a_0}\right) \quad (9)$$

where $d_0, d_1, d_2 > 0$, and f satisfies

$$\begin{aligned} f &\in C^3(\mathbf{R}, (0, 1)), \\ f'(x) &< 0 \quad \forall x \in \mathbf{R}, \\ \lim_{x \rightarrow -\infty} f(x) &= 1, \quad \lim_{x \rightarrow \infty} f(x) = 0, \quad \lim_{x \rightarrow \infty} f'(x) = 0. \end{aligned} \quad (10)$$

An example of a function f satisfying these properties is $f(x) = 1/2 - (1/\pi) \arctan(\alpha_f x)$.

The assumptions above deal with immediate effects of stress and coping behaviour. Given the complexity of the interaction between stress and the endocrine system, there could be cumulative effects of stress on birth and death rates that are not accounted for by these assumptions. Although the general approach could be modified to handle other effects, in this study we assume that all other effects are higher order and can be ignored.

The ‘fitness generating function’ [44] is defined as the per capita growth rate $(1/N)dN/dt$, which is, in our case,

$$G(\boldsymbol{\beta}, N) = a(\boldsymbol{\beta}) - c(\boldsymbol{\beta}) - d(\boldsymbol{\beta})N. \quad (11)$$

The Darwinian dynamics model is specified by Equations (5)–(11). If the covariances in Equation (5) are small relative to the variances, we might assume $\delta_{ij} = 0$. In Appendix 1, we prove the following lemma.

LEMMA 1 *Let $\delta_{ij} = 0$. Then the equilibria of Equations (5)–(11) for which $N \geq 0$ have the form $(N^*, \alpha_1, \alpha_2, \dots, \alpha_{n-1}, \beta_n^*)$, and these equilibria are stable in the direction of each β_i for $i = 1, 2, \dots, n - 1$.*

Lemma 1 implies that, in phase space, all solutions approach the $N - \beta_n$ plane. To analyse the equilibrium dynamics, we therefore can restrict our attention to the $N - \beta_n$ plane after setting $\beta_i = \alpha_i$ for $i = 1, 2, \dots, n - 1$. Using this approach in Appendix 1, we prove the following theorem.

THEOREM 2 *Let $\delta_{ij} = 0$ and $c_0 = d_2 = 0$. Then*

- (1) $(0, \alpha_1, \alpha_2, \dots, \alpha_{n-1}, 0)$ is an equilibrium of Equations (5)–(11), and it is unstable.
- (2) All other equilibria, of which there exists at least one, are strictly positive.

Theorem 2 addresses a special case in which (1) comfort preening does not increase predation risk ($c_0 = 0$), and (2) compromised health due to comfort preening does not affect density-dependent mortality ($d_2 = 0$). From a mathematical point of view, the special case in Theorem 2 provides a baseline from which we can obtain more general results.

Finally, in Appendix 1 we prove that certain constraints on f guarantee the existence of a unique positive equilibrium that is stable.

THEOREM 3 *Let $\delta_{ij} = 0$ and $c_0 = d_2 = 0$. Suppose $f''(0) = 0$ and $f''(x) > 0$ for all $x > 0$. Suppose further that $\ln(d_0 + d_1 f(u))$ has a unique inflection point at some $\hat{u} \in R$ and that $f'(\hat{u})f'''(\hat{u}) \neq f''(\hat{u})f''(\hat{u})$. Then for all sufficiently large $\sigma_n > 0$ there exists a unique positive equilibrium of Equations (5)–(11) and this equilibrium is stable.*

Theorem 3 guarantees that, for a special case, there is a positive stable state to which coping behaviour can evolve. Simulations suggest that this situation is fairly robust in the general case, as well. In our application we use $f(x) = 1/2 - (1/\pi) \arctan(\alpha_f x)$, which satisfies the conditions in Theorem 3.

3. Estimation of logistic regression model for preening

In this section, we identify environmental correlates for preening in seabirds and quantify the response of preening to changes in these correlates. That is, our goal in this section is to specify the logistic regression model (1) and estimate its parameters.



Figure 1. Sample Areas A–E in the colony on Violet Point and the observation point at the west end atop the 33 m bluff. The larger colony extends throughout most of the spit.

3.1. Data

We collected data on preening behaviour at Protection Island National Wildlife Refuge (48°08'N, 122°55'W), Jefferson County, Washington, USA. The island lies at the southeast corner of the Strait of Juan de Fuca, and consists mostly of a high plateau bordered by steep bluffs. Violet Point, a gravel spit extending to the southeast, contains a breeding colony of more than 2400 pairs of nesting glaucous-winged gulls. We selected five rectangular sample subareas in the colony (Figure 1, Areas A–E). The combined sample area measured 4205 m² and contained 259 and 238 nests with eggs in 2006 and 2007, respectively. The larger colony extends throughout most of the spit.

Hourly behaviour scans were taken from 5.00 a.m. to 8.00 p.m. Pacific Standard Time (PST) using a 20–60× spotting scope from the observation point atop a 33 m bluff that borders the west end of the spit (Figure 1). At the top of each hour, the behaviour of each bird in the sample area was recorded by voice and subsequently transcribed. The usual procedure was to scan all birds in a sample area. If the area contained more than 50 birds, however, the scan typically was terminated after the first 50. The scans were conducted during three stages of the reproductive season: 19–29 May 2006 during the ‘nest-building/egg-laying’ stage; 13–21 and 23 June 2006 during the ‘egg-laying/incubation’ stage; and 10–13 and 15–19 July 2007 during the ‘incubation/chick-rearing’ stage.

We obtained solar elevations and tide heights from the National Oceanic and Atmospheric Administration (NOAA). A weather station located 2 m above site elevation on the northwest end of Violet Point recorded hourly values of relative humidity, temperature, wind speed, and barometric pressure. No measurable rainfall was recorded during our data collection period.

3.2. Logistic regression analysis

We considered preening as a function of $x_1 = \text{HUM}$ (relative humidity as a percent), $x_2 = \text{TEMP}$ (ambient temperature in degree Celsius), $x_3 = \text{SUN}$ (solar elevation measured as degrees above

Table 1. Coding of design variables for STAGE, coded at three levels.

| Data collection period | Stage | D_{71} | D_{72} |
|------------------------|--------------------------|----------|----------|
| 19–29 May 2006 | Nest-building/egg-laying | 0 | 0 |
| 13–21, 23 June 2006 | Egg-laying/incubation | 1 | 0 |
| 10–13, 15–19 July 2007 | Incubation/chick-rearing | 0 | 1 |

Note: Nest-building/Egg-laying period is the reference stage.

the horizon), $x_4 = \text{WIND}$ (wind speed on the colony in m/sec), $x_5 = \text{TIDE}$ (tide height in m), $x_6 = \text{BAR}$ (barometric pressure in mmHg), and the STAGE of breeding season (using two design variables D_{71} and D_{72} coded at three levels; Table 1). The global model included the 12 interactions between the environmental variables and the design variables:

$$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \sum_{j=1}^6 \beta_j x_j + \sum_{k=1}^2 \beta_{7k} D_{7k} + \sum_{k=1}^2 \sum_{j=1}^6 \beta_{jk} x_j D_{7k}, \quad (12)$$

where the dependent variable p is the probability of preening.

Model (12) is a global model that includes all submodels in which various coefficients are set to zero; model (12) and its ‘nested’ submodels can be viewed as a suite of alternative hypotheses. We took an information-theoretic approach [2] to model selection and parameter estimation. In particular, we used the Akaike Information Criterion (AIC), adjusted for overdispersion, to rank the nested models. (Overdispersion occurs when the sampling variance exceeds the theoretical variance and can result from a lack of independence in individual responses. Non-independence of observations is a common problem with behaviour scans because different scans may or may not include some of the same animals.) We also ranked the factors HUM, TEMP, SUN, WIND, TIDE, and BAR in order of importance using Akaike weights [2, p. 168]. Details appear in Appendix 2.

The best model ($\Delta\text{AIC} = 0$) for the entire data set was the global model (12); there were four other models with $\Delta\text{AIC} < 10$ (Table 2). The overdispersion parameter estimate from the global model ($\hat{\tau} = 1.95$; $\text{df} = 2371$) was well within the range of values (1–4) that indicate a small amount of extrabinomial variation (due to demographic stochasticity and lack of independence) rather than inadequate model structure [2, p. 67]. The model-averaged coefficients are shown in Table 3, along with unconditional standard errors and model-averaged correlation coefficients. Odds-ratios and 95% confidence intervals are listed in Table 4. The Akaike weight analysis of which factors were ‘more important’ is summarized in Table 5. The most important factors identified by the Akaike weights (Table 5) are the same as the factors shown to have significant effect on the odds ratio (Table 4).

Results of the regression analysis show that changes in the abiotic environment of glaucous-winged gulls significantly correlate with the incidence of preening. Over the entire breeding season, all factors – stage of breeding season, solar elevation, humidity, tide height, wind speed,

Table 2. Summary of AIC statistics for the five models with $\Delta < 10$.

| Model | QAIC _c | Δ_i | w_i |
|--------------|-------------------|------------|-------|
| Global | 41710.723 | 0 | 0.767 |
| Without BAR | 41714.988 | 4.264 | 0.091 |
| Without TEMP | 41715.086 | 4.363 | 0.087 |
| Without WIND | 41716.776 | 6.052 | 0.037 |
| Without TIDE | 41719.027 | 8.304 | 0.012 |

Note: Second-order Akaike Information Criterion for overdispersed data (QAIC_c); QAIC_c differences (Δ_i); and Akaike weights (w_i).

Table 3. Model averaged estimates for global model.

| Term | Coefficient | SE | \bar{r} |
|-----------------------------------|-------------|--------|-----------|
| β_0 | 0.8497 | 5.641 | |
| β_1 HUM | 0.0283 | 0.0093 | |
| β_2 TEMP | -0.1353 | 0.0454 | |
| β_3 SUN | -0.0008 | 0.0020 | |
| β_4 WIND | -0.0336 | 0.0283 | |
| β_5 TIDE | 0.0701 | 0.0462 | |
| β_6 BAR | -0.0051 | 0.0075 | |
| β_{71} D_{71} | 1.338 | 7.851 | |
| β_{72} D_{72} | 20.59 | 12.05 | |
| β_{11} HUM $\times D_{71}$ | -0.0226 | 0.0103 | -0.9061 |
| β_{21} TEMP $\times D_{71}$ | 0.1477 | 0.0499 | -0.9095 |
| β_{31} SUN $\times D_{71}$ | -0.0056 | 0.0025 | -0.8096 |
| β_{41} WIND $\times D_{71}$ | 0.0545 | 0.0361 | -0.7744 |
| β_{51} TIDE $\times D_{71}$ | -0.0127 | 0.0535 | -0.8648 |
| β_{61} BAR $\times D_{71}$ | -0.0004 | 0.0107 | -0.7053 |
| β_{12} HUM $\times D_{72}$ | -0.0131 | 0.0110 | -0.8890 |
| β_{22} TEMP $\times D_{72}$ | 0.1594 | 0.0501 | -0.9154 |
| β_{32} SUN $\times D_{72}$ | -0.0013 | 0.0024 | -0.8318 |
| β_{42} WIND $\times D_{72}$ | -0.0670 | 0.0428 | -0.6510 |
| β_{52} TIDE $\times D_{72}$ | 0.0008 | 0.0532 | -0.8713 |
| β_{62} BAR $\times D_{72}$ | -0.0303 | 0.0136 | -0.5528 |

Notes: Coefficient estimates are averages of the maximum likelihood (ML) coefficients over all models; unconditional standard error (SE) estimates include information from all models containing the parameter, and incorporate model uncertainty; correlation coefficient estimates (\bar{r}) are model-averaged over models containing the interaction terms. $n = 79, 286$.

Table 4. Odds-ratios (OR) and 95% confidence intervals (CI).

| Factor | c | OR | 95% CI |
|--|-----|------|------------------|
| Nest-building/egg-laying stage ($D_{71} = D_{72} = 0$) | | | |
| HUM ^a | 20 | 1.8 | (1.223, 2.533) |
| TEMP ^a | 5 | 0.51 | (0.3258, 0.7936) |
| SUN | 60 | 0.95 | (0.7551, 1.205) |
| WIND | 5 | 0.85 | (0.6405, 1.115) |
| TIDE | 3 | 1.2 | (0.9407, 1.619) |
| BAR | 10 | 0.95 | (0.8203, 1.102) |
| Egg-laying/incubation stage ($D_{71} = 1$ and $D_{72} = 0$) | | | |
| HUM | 20 | 1.1 | (0.9446, 1.328) |
| TEMP | 5 | 1.1 | (0.8683, 1.304) |
| SUN ^a | 60 | 0.68 | (0.5753, 0.8075) |
| WIND | 5 | 1.1 | (0.8872, 1.389) |
| TIDE ^a | 3 | 1.2 | (1.014, 1.391) |
| BAR | 10 | 0.95 | (0.8165, 1.098) |
| Incubation/chick-rearing stage ($D_{71} = 0$ and $D_{72} = 1$) | | | |
| HUM ^a | 20 | 1.4 | (1.111, 1.648) |
| TEMP | 5 | 1.1 | (0.9260, 1.375) |
| SUN | 60 | 0.88 | (0.7535, 1.031) |
| WIND ^a | 5 | 0.60 | (0.4397, 0.8312) |
| TIDE ^a | 3 | 1.2 | (1.061, 1.442) |
| BAR ^a | 10 | 0.70 | (0.5618, 0.8774) |

Notes: c is the unit of increase in the variable that generates the OR. For Nest-building/egg-laying stage, $n = 13, 384$; for egg-laying/incubation stage, $n = 35, 505$; for incubation/chick-rearing stage, $n = 30, 397$.

^aEffect of the variable is significant.

Table 5. Relative variable importance.

| NE | w_+ | EI | w_+ | IC | w_+ | All | w_+ |
|-------------------|-------|-------------------|-------|-------------------|-------|--------------------|---------|
| TEMP ^a | 0.993 | SUN ^a | 1.000 | BAR ^a | 0.989 | STAGE ^a | 1.00000 |
| HUM ^a | 0.986 | TIDE ^a | 0.875 | HUM ^a | 0.987 | SUN ^a | 0.99988 |
| TIDE | 0.668 | HUM | 0.660 | WIND ^a | 0.980 | HUM ^a | 0.99979 |
| WIND | 0.437 | BAR | 0.528 | TIDE ^a | 0.972 | TIDE ^a | 0.98587 |
| SUN | 0.318 | TEMP | 0.339 | SUN | 0.498 | WIND ^a | 0.95850 |
| BAR | 0.312 | WIND | 0.329 | TEMP | 0.358 | TEMP ^a | 0.91156 |
| | | | | | | BAR ^a | 0.90538 |

Notes: Evidence for the importance of each variable is based on sums of Akaike weights (w_+) over models in which the variable occurs. Factors are listed in decreasing order of importance for the nest-building/egg-laying stage (NE), egg-laying/incubation stage (EI), incubation/chick-rearing stage (IC), and the entire breeding season (All). For each stage the calculations were based on an overdispersion parameter estimate from the data for that stage (NE $\hat{\tau} = 1.86$; EI $\hat{\tau} = 1.91$; IC $\hat{\tau} = 2.08$).

^aSignificant variables are arbitrarily designed as those with $w_+ > 0.7$.

temperature, and barometric pressure – were important for predicting the likelihood of preening. The stage of breeding season was the most important factor, and, depending on the stage of the breeding season, two to four other factors were relatively important.

Note that non-significance of a factor in Table 4 does not imply that the corresponding term in Table 3 can be eliminated from the model. For example, the fact that humidity is not significant during the egg-laying/incubation stage does not allow us to remove the term $\beta_{11}\text{HUM} \times D_{71}$ from the regression model. To see why this is true, consider the three humidity terms with coefficient estimates from Table 3:

$$0.0283 \times \text{HUM} - 0.0226\text{HUM} \times D_{71} - 0.0131 \times \text{HUM} \times D_{72}. \quad (13)$$

Note that when $D_{71} = 1$ and $D_{72} = 0$ (egg-laying/incubation stage), the combined coefficient on HUM is close to zero, which comports with the fact that humidity is not a significant factor during that stage. The middle term is required to ‘cancel out’ the first term. Thus, no term may be deleted from the global regression model (12).

The logistic regression results can be summarized by season as follows. During the nest-building/egg-laying stage, the odds of preening increased 80% with each 20 percentage points increase in relative humidity, but decreased 49% with each 5° increase in temperature. During the egg-laying/incubation stage, the odds of preening increased 20% at a high tide when compared with a low tide, but decreased 32% at midday ($\text{SUN} = 60^\circ$) from sunrise/sunset. During the incubation/chick-rearing stage, the odds of preening increased 40% with each 20 percentage point increase in humidity, and 20% at a high tide compared with a low tide; it decreased 40% with each 5 m/s rise in wind speed, and 30% with each 10 mmHg rise in barometric pressure.

4. Simulation of the Darwinian dynamics model for comfort preening

The logistic regression model (12) contains 20 regression coefficients not counting the intercept. The Darwinian dynamics model (5) therefore consists of 22 coupled differential equations: one for the population size N , 20 for the non-comfort preening regression coefficients $\beta_1, \beta_2, \dots, \beta_{n-1}$, and one for the coefficient of comfort preening β_n . In this section, we discuss a typical numerical simulation of model (5) in order to suggest whether and how comfort preening might invade the system.

Figure 2 shows the hypothetical evolution of preening in the absence and then in the presence of stress when the population size is initially small and all preening coefficients are initially zero. Here, we set the parameters α_i in Equation (7), which denote the optimal values of the preening

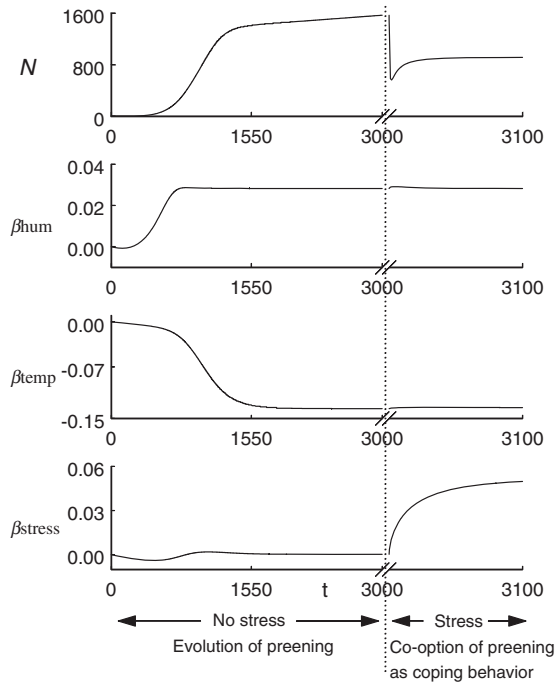


Figure 2. Simulation of model (5)–(11) with the behaviour coefficients from model (12). The initial population size is $N(0) = 5$ and all preening coefficients are initially zero. For $t = 0$ –3000 stress is set to zero ($c_0 = d_1 = 0$). The population size N approaches the carrying capacity, the 20 non-comfort preening coefficients (of which only β_{hum} and β_{temp} are shown) approach their optimal values given in Table 3, and the comfort preening coefficient β_{stress} approaches zero. For $t = 3000$ –3100 the population is stressed ($c_0 = 0.0005$, $d_1 = 0.005$). The population size drops and then rises to a lower carrying capacity than before, the non-comfort preening coefficients return to their optimal values, and the comfort preening coefficient approaches a positive limit. The other parameters are $a_0 = 3$, $d_0 = d_2 = c_0 = 0.0005$, $s_i = 0.01$, $\delta_{ij} = 0.005$. We used $h(x) = 1/2 + (1/\pi) \arctan(70x)$ and $f(x) = 1/2 - (1/\pi) \arctan(80x)$ in Equations (8) and (9). The optimal values α_i for the non-comfort preening coefficients in Equation (7) are set to the estimated coefficients in Table 3, and the σ_i for the non-comfort preening coefficients were set to $\sigma_i = |\alpha_i|$. The σ_{stress} for comfort preening (σ_n in Equation (7)) is $\sigma_{\text{stress}} = 0.1$.

coefficients, equal to the values in Table 3 that were estimated empirically from the Protection Island colony. The other parameters are given in the caption of Figure 2.

During time $t = 0$ –3000, stress is set to zero ($c_0 = d_1 = 0$). The population size approaches carrying capacity and the non-comfort preening coefficients approach their optimal values. Here, we show only β_{hum} and β_{temp} , the coefficients on humidity and temperature, which approach the values shown in Table 3 (0.0283 and -0.1353 , respectively). The comfort preening coefficient β_{stress} fluctuates due to the covariances $\delta_{ij}^2 > 0$ in model (5), and then approaches its non-stressed optimal value of zero. That is, in the absence of stress, comfort preening does not invade the system.

At time $t = 3000$ in Figure 2, stress is initiated in the population by setting $c_0, d_1 > 0$. This represents the advent of predator disturbances due to rapidly rebounding eagle populations. At this point, the comfort preening coefficient β_{stress} begins to increase, and the non-comfort preening coefficients fluctuate slightly from their optimal values. The population size drops and then rises to a new carrying capacity that is lower than before. The non-comfort preening coefficients return to their optimal values and the coefficient β_{stress} approaches a positive value (≈ 0.05). That is, in the presence of stress, comfort preening is predicted to invade the system.

Thus, model (5)–(11) predicts that the extant behaviour of preening will be co-opted as a coping behaviour given the increased level of eagle activity. If the limiting value $\beta_{\text{stress}} \approx 0.05$ is

interpreted as a regression coefficient for a binary factor STRESS (taken to be 1 if there is an eagle disturbance, and 0 otherwise), the odds ratio is $e^{0.05} \approx 1.05$, and hence the odds of preening are predicted to be 5% greater after an eagle disturbance than before. This value depends, of course, on the values of the parameters, in particular, the value of σ_{stress} , shown as σ_n in Equation (7). In this study, we did not have estimates of the σ_i , so the 5% prediction is qualitative rather than quantitative.

5. Independent test for comfort preening

In this section, we present an independent test of whether gulls in the Protection Island colony use preening as a coping behaviour after eagle disturbances.

Eagles commonly perch on Refuge signs and beach logs at the east end of Violet Point (where there is a harbour seal, *Phoca vitulina*, rookery) and on the 33 m bluff bordering the west end of Violet Point (Figure 1). Flights along the length of the spit between these two locations cause disturbances in the gull colony below. The number of such disturbances has risen sharply with rebounding eagle populations. During our work in the 1980s, few eagle disturbances were observed each day on Violet Point. During a single day in 1995, however, we observed 213 eagle flights over the spit [23].

From the observation point atop the bluff, one can see the approach of a west-bound eagle and monitor the disturbance of the gull colony as the disturbance advances in a wave along the spit towards the observer. The onset of disturbance is indicated by the ‘upright alert’ posture of individual gulls and is followed by increased sound levels due to long calls. Gulls along the direct path of a disturbance may take flight, while those on the periphery remain on their territories. If the eagle(s) stoops into the colony, an intense spit-wide disturbance can result with the majority of the colony taking flight in a massive cyclonic pattern [23].

Five digital video cameras, mounted together in a blind at the observation point and linked to operate in synchrony, recorded the behaviours of gulls in the five sample areas during eagle disturbances. The observation point was located 100 m from the proximal edge of the colony, and more than 100 m from each sample area. When the observer saw that an eagle was flying towards the colony, all five cameras were activated and simultaneously recorded the behaviours of gulls before, during, and after the disturbance. The onset of disturbance for a given sample area was defined as the time at which the gulls in that sample area that were closest to the approaching eagle first assumed the upright alert posture.

It was difficult to anticipate a disturbance before it actually occurred, and most recordings had to be eliminated, either because the eagle changed course and the disturbance failed to materialize, or because the recording was started too late and some of the five sample areas were already disturbed at the beginning of the clip. The two videos usable for this analysis were recorded at 11.00 a.m. and 2.30 p.m. PST on 17 June 2006.

For each recorded bald eagle disturbance, we counted the total number of gulls in each sample area and the number of gulls preening in that area from the videos. Counts were made at the beginning of each 15-s interval. One-tailed paired *t*-tests at the 0.05 significance level were used to compare the average frequencies of preening before and after the disturbances in sample areas, in order to test the null hypothesis that the frequency of preening in each area was no higher after the disturbance than before.

The 11.00 a.m. PST disturbance was essentially colony-wide; 94% (171 of 182) gulls fled Areas A–E (Figure 3(a)). The mean proportion of gulls preening at 15-s intervals during the 2-min period just before the disturbance was taken as the ‘before’ preen frequency for each sample area. Three minutes after the beginning of the disturbance, virtually all residents had returned to

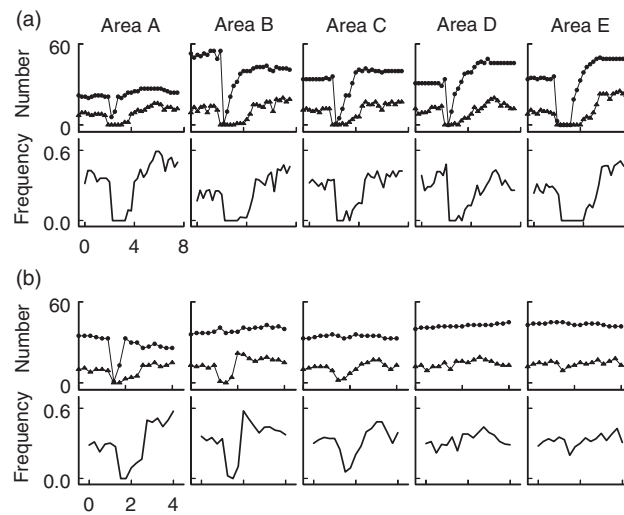


Figure 3. Observed occupancies (circles), numbers of gulls preening (triangles), and preening frequency (line) before, during, and after eagle disturbances in the five sample areas. (a) Disturbance recorded at 11.00 a.m. PST on 17 June 2006. (b) Disturbance recorded at 2.30 p.m. PST on 17 June 2006.

their territories and the mean proportion of gulls preening at 15-s intervals during the next 2 min was taken as the ‘after’ preen frequency for that sample area. The mean (\pm SD) preen frequency averaged over all five sample areas was significantly higher (paired $t = 2.80$, 4 df, $P = 0.02$) for ‘after’ ($\bar{X} = 0.41 \pm 0.07$) than ‘before’ ($\bar{X} = 0.31 \pm 0.06$).

The 2.30 PST disturbance was localized over Area A; 97% (32 of 33) gulls flew from Area A, but only 3% (5 of 164) gulls fled Areas B–E (Figure 3(b)). Because of the large difference in response intensity between gulls in Area A and those in Areas B–E, Area A data were eliminated from the t -test comparison. This allowed us to determine if ‘before’ and ‘after’ preen frequency changed even for gulls that remained on territory during a disturbance. Also, because most of the gulls in Areas B–E did not fly, they could resume preening earlier than gulls that fled. We captured only 1 min 45 s of video before the beginning of the second disturbance, so the mean ‘before’ frequency for the second disturbance was calculated in the same way as for the first disturbance except based on the shorter sample period of 1 min 45 s. One minute after the beginning of the disturbance, the mean proportion of gulls preening at 15-s intervals during the next 2 min was taken as the ‘after’ preen frequency for that sample area. The mean (\pm SD) preen frequency averaged over all four sample areas was significantly higher (paired $t = 2.98$, 3 df, $P = 0.03$) for ‘after’ ($\bar{X} = 0.37 \pm 0.02$) than ‘before’ ($\bar{X} = 0.31 \pm 0.03$). Note that the odds of preening after the disturbance were $\bar{X}/(1 - \bar{X}) \approx 0.59$, whereas the odds of preening before the disturbance were approximately 0.45. Thus, the odds of preening were 31% greater after the disturbance than before.

Area A was about 17 m from the proximal edge of the next closest sample area and was not continuously connected by territories to any of Areas B–E (Figure 1). This suggests that the increased preening in Areas B–E during the second disturbance was not socially facilitated by the increase in Area A.

Gulls frequently preen after flight, presumably to rearrange flight feathers [17]; hence, increased preening after disturbances in which birds take flight is not surprising. These results, however, give the first demonstration of increased preening in birds that were alerted to a predator but did not take flight. This finding is both consistent with and supportive of the hypothesis that gulls utilize preening as a coping behaviour.

6. Discussion

This study makes four contributions: (1) the combination of two existing modelling approaches – logistic regression and Darwinian dynamics – to create a method for modelling the microevolution of animal behaviour, and the use of this method to explore theoretically the selective advantage of coping behaviour, (2) a study of the environmental correlates of preening behaviour in glaucous-winged gulls, (3) an application of the modelling methodology to investigate whether and how preening might evolve as a coping behaviour, and (4) an independent field test of whether preening might function as a coping behaviour.

A number of caveats and comments deserve attention.

6.1. Inferential

The most important caveats relate to inferences about causation and function. This is the first study to demonstrate and measure increased preening in birds that were alerted to a predator but did not take flight. Although this result is supportive of the hypothesis that gulls use preening as a coping behaviour, it is by no means conclusive. The result does not establish a proximal causal link between disturbance and preening, and in any event, the psychological state of the bird is unknown. Even if preening were demonstrated to serve as a coping behaviour, it could be a learned response to stress rather than an evolutionary adaptation. Recent work, however, has shown a strong genetic basis for the frequency of grooming behaviour in mice [6], and this is probably true for birds as well.

Also, we note that the environmental correlates identified in the logistic regression analysis may or may not be drivers for preening.

6.2. Mathematical

Although the logistic regression model (1) is probably a fairly accurate way to quantify behaviour, the logistic population model (4) is likely a crude proxy for gull population dynamics. A better population model would account for specifics of life history, for example, the fact that glaucous-winged gulls mature after 4 years. Also, stress and coping behaviour probably have cumulative effects on fitness, whereas we included only immediate effects in the population model, assuming that other effects were of higher order and could be ignored. Furthermore, our model assumes the population is ‘closed’, with no immigration. Banding studies from the 1980s showed that dispersion from the Protection Island colony was primarily to the other locations in the Salish Sea (the inland marine waters of northwest Washington), and likewise, that nearly all of the immigration into the Protection Island colony came from birds banded at other locations in the Salish Sea. For chicks hatched on Protection Island, movement back to the natal colony began at 3–4 years of age. Thus, we suspect the assumption of a closed population is fairly accurate for the larger population occupying the waters of the Strait of Juan de Fuca, Strait of Georgia, and Puget Sound area [35].

In our simulations, we considered an unrealistically abrupt onset of eagle disturbances (Figure 2) by setting $c_0 = d_1 = 0$ for times $t = 0$ –3000 and then setting $c_0, d_1 > 0$ at time $t = 3000$. In future work, we will consider a predator–prey model for gulls and eagles in which the coefficients c_0 and d_1 are functions of eagle numbers.

Another mathematical caveat concerns the fact that Darwinian dynamics assumes the trait variances s_i^2 and covariances δ_{ij}^2 are constant across time. This may not be true in some situations, for example, after a population bottleneck. It seems feasible that the trait variances and covariances could be estimated directly from the population in order to test this assumption and to approximate the speed of evolution.

6.3. Biological

A complete analysis of preening as a function of environmental factors must include the effect of rain. Protection Island is situated within the driest isocline of the rain shadow of the Olympic Mountains [28, p. 40]. Rainfall during our data collection period was infrequent, episodic, and unmeasurable by the weather station, and hence was not used in the logistic regression analysis. The occurrence of rain, however, was noted by the observers in the field. We analysed its effect by comparing the mean frequency of preening during rain, during the hour before rain, during the hour after rain, and during hours on days with no rain. Mean frequencies were compared using a one-way ANOVA and a Bonferonni's multiple comparison test carried out at the 0.05 significance level. The mean (\pm SD) proportions of gulls preening during rain hours ($\bar{X} = 0.21 \pm 0.16$, $N = 41$) with hours directly before rain ($\bar{X} = 0.12 \pm 0.08$, $N = 24$), hours directly after rain ($\bar{X} = 0.15 \pm 0.11$, $N = 30$), and hours on days with no rain ($\bar{X} = 0.17 \pm 0.01$, $N = 503$) were significantly different ($F = 3.127$, 3 df, 597, $P = 0.0254$) on the basis of square root-transformed data. Moreover, the post hoc test showed that the mean proportion of preening was higher for rain hours than for hours before rain.

We also note that the data for this study were collected over two different years, one of which (2007) was during an El Niño event. Unfortunately, we were unable to consider the effect of year in the regression analysis because the 2007 data set and the incubation/chick-rearing data set were the same. It is therefore possible that some results ostensibly linked to the incubation/chick-rearing stage were actually due to the effects of El Niño. After collecting behaviour data on this colony during several decades including a number of El Niño events, however, we suspect that, although feeding and reproductive behaviours are impacted during El Niño events, maintenance behaviours (given that a bird is on the colony and experiencing a given suite of environmental conditions) probably are not affected greatly.

Furthermore, our study did not address the function of preening in relation to removal of ectoparasites. Clayton *et al.* [12] review numerous studies that show that preening serves as 'a critical defense against ectoparasites'. We hope to examine the effect of ectoparasite removal on preening frequency in future modelling studies. In this regard, it is interesting to note that gulls exhibit 'bill overhang' [12, Table 1], a structural feature associated with especially effective removal of parasites during preening [9,11].

Finally, we note that the independent test for comfort preening, being a 'natural experiment', yielded only two disturbances which could be analysed, even though the observers spent many full days at the observation point recording disturbances. We point out, however, that the number of gulls was large.

6.4. Conclusion

In this paper, data and theory are somewhat integrated but not rigorously so: first, we were not able to estimate rigorously all of the model parameters; second, the functional effects of behaviour on population dynamics and fitness were hypothetical and not measured; and third, the population model itself was extremely simplified from a biological point of view. Nevertheless, we hope that the partial integration of data and theory provides a tool to probe the possible effects of stress on the evolution of coping behaviour and gives insight into how studies of this type might be accomplished with greater rigor.

We note that there are many scientific studies in a variety of fields in which logistic regression is used to connect binary outcomes with associated factors. This is particularly true in epidemiology; the literature is full of studies that include estimates of regression coefficients. In some cases, regression coefficients may be subject to natural selection. We, therefore, hope that the general

framework presented in this paper may find application beyond behavioural ecology to a wide range of other disciplines.

Acknowledgements

We thank Kevin Ryan, project leader for the Washington Maritime National Wildlife Refuge Complex, U.S. Fish and Wildlife Service, for permission to work on Protection Island National Wildlife Refuge; Brian Dennis, Joseph Galusha, and John Berez for discussions; Cassandra Boothby for help with data collection; Jerry Weldon for programming assistance; and two anonymous referees. Rosario Beach Marine Laboratory provided logistical support. This research was supported by Andrews University faculty grants and U.S. National Science Foundation grants DMS 0314512 and DMS 0613899 (S.M.H. and J.L.H.). D.J.G. participated in this research as an undergraduate member of the Andrews University Honors Program.

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Appendix 1

Proof of Lemma 1 Let $\delta_{ij} = 0$. From Equations (5)–(11), it is straightforward to show that the equilibrium equations for β_i , $i = 1, 2, \dots, n - 1$, are

$$\frac{d\beta_i}{dt} = -s_i^2 a(\beta) \left(1 + \frac{d_2}{a_0} N \right) \left(\frac{\beta_i - \alpha_i}{\sigma_i^2} \right) = 0. \quad (\text{A1})$$

Given $N \geq 0$, this implies $\beta_i = \alpha_i$ for $i = 1, 2, \dots, n - 1$. Also, β_i increases (decreases) whenever $\beta_i < \alpha_i$ ($\beta_i > \alpha_i$). ■

Proof of Theorem 2 Let $\delta_{ij} = 0$ and $c_0 = d_2 = 0$. Let u , σ , and s designate β_n , σ_n , and s_n , respectively. By Lemma 1, together with Equations (5)–(11), the equilibria of Equation (5) and their stabilities are determined by those of the two-dimensional system

$$\begin{aligned} \frac{dN}{dt} &= a_0 e^{-1/2(u/\sigma)^2} N - (d_0 + d_1 f(u)) N^2, \\ \frac{du}{dt} &= -s^2 \left(a_0 \left(\frac{u}{\sigma^2} \right) e^{-1/2(u/\sigma)^2} + d_1 f'(u) N \right). \end{aligned} \quad (\text{A2})$$

Clearly (0, 0) is an equilibrium of (A2) and is the only equilibrium with $N = 0$. The Jacobian of Equation (A2) at (0, 0) has the form

$$J = \begin{pmatrix} a_0 & 0 \\ J_{21} & -\frac{s^2 a_0}{\sigma^2} \end{pmatrix}, \quad (\text{A3})$$

which implies that (0, 0) is a saddle with a stable manifold on the u -axis.

The equations for non-trivial equilibria ($N > 0$) of Equation (A2) can be written

$$N = \frac{a_0 e^{-1/2(u/\sigma)^2}}{d_0 + d_1 f(u)} \tag{A4}$$

and

$$N = \frac{-a_0(u/\sigma^2)e^{-1/2(u/\sigma)^2}}{d_1 f'(u)}. \tag{A5}$$

Equations (A4) and (A5) together imply that non-trivial equilibria (N^*, u^*) are determined by solutions of

$$H(u) = \frac{-u}{\sigma^2}, \tag{A6}$$

where H is defined as

$$H(u) \equiv \frac{d_1 f'(u)}{d_0 + d_1 f(u)}. \tag{A7}$$

Given the properties of f assumed in Equation (10), it is clear that $H(u)$ is a negative C^2 function that approaches zero as $u \rightarrow \infty$. Therefore, the curve $y = H(u)$ intersects the line $y = -u/\sigma^2$ for at least one point $u^* > 0$, and there are no intersections for $u \leq 0$. At each intersection, the equilibrium value $N^* > 0$ can be computed from Equation (A4) or Equation (A5). ■

Proof of Theorem 3 Let $\delta_{ij} = 0$ and $c_0 = d_2 = 0$. Suppose $f''(0) = 0$ and $f''(x) > 0$ for all $x > 0$. Suppose further that $\ln(d_0 + d_1 f(u))$ has a unique inflection point at $\hat{u} \in R$ and that $f'(\hat{u})f'''(\hat{u}) \neq f''(\hat{u})f''(\hat{u})$.

Let H be defined as in Equation (A7). The first goal is to show that the intersection guaranteed in the proof of Theorem 2 is unique for sufficiently large σ . Note that the first derivative of $\ln(d_0 + d_1 f(u))$ is $H(u)$. The assumption that $\ln(d_0 + d_1 f(u))$ has a unique inflection point at $\hat{u} \in R$ is equivalent to the assumption that its second derivative H' changes sign exactly once – at $\hat{u} \in R$. Given the assumption $f''(0) = 0$, it is easy to check that $H'(0) < 0$. Also, $H(0) < 0$ and $\lim_{u \rightarrow \infty} H(u) = 0$ by the properties of f given in Equation (10). Since H is decreasing from a negative value at $u = 0$, but eventually must increase towards zero, the change in sign of H' must occur at a positive number $\hat{u} > 0$, and H must be decreasing on $(-\infty, \hat{u})$ and increasing on (\hat{u}, ∞) .

Let σ be large enough so that

$$\sigma^2 > \max_{u \in [0, \hat{u}]} \left\{ -\frac{u}{H(u)} \right\}; \tag{A8}$$

this is possible by the Extreme Value Theorem. Then $-u/\sigma^2 > H(u)$ for all $u \in [0, \hat{u}]$, and in particular, this inequality holds at $u = \hat{u}$. On the interval (\hat{u}, ∞) , the line $y = -u/\sigma^2$ is decreasing and the curve $y = H(u)$ is increasing; consequently, there exists a unique intersection at some $u^* > \hat{u}$ for which $-u^*/\sigma^2 = H(u^*)$. From Equations (A4)–(A6), we obtain a unique positive equilibrium (N^*, u^*) .

The next goal is to prove that this equilibrium is stable. It is straightforward to check that

$$H'(u) = 0 \iff H(u) = \frac{f''(u)}{f'(u)}. \tag{A9}$$

Thus, the curve $y = f''(u)/f'(u)$, which passes through the origin by the assumption $f''(0) = 0$, intersects the curve $y = H(u)$ at exactly one point, namely at the minimum $(\hat{u}, H(\hat{u}))$ of H . The assumption that $f'(\hat{u})f'''(\hat{u}) \neq f''(\hat{u})f''(\hat{u})$ guarantees that this intersection is not tangential, because it implies that the derivative of f''/f' is nonzero at the intersection. Thus, we have $H < f''/f'$ on $(0, \hat{u})$ and $H > f''/f'$ on (\hat{u}, ∞) . Because $u^* > \hat{u}$, this implies that

$$H(u^*) > \frac{f''(u^*)}{f'(u^*)}. \tag{A10}$$

The Jacobian of Equation (A2) has an upper left-hand entry

$$J_{11} = a_0 e^{-1/2(u/\sigma)^2} - 2(d_0 + d_1 f(u))N. \tag{A11}$$

By Equation (A4), at equilibrium this reduces to

$$J_{11} = -a_0 e^{-1/2(u^*/\sigma)^2} < 0. \tag{A12}$$

The upper right-hand entry is

$$J_{12} = -\left(\frac{u}{\sigma^2}\right) a_0 e^{-1/2(u/\sigma)^2} N - d_1 f'(u)N^2. \tag{A13}$$

By Equation (A5), this becomes $J_{12} = 0$ at the equilibrium. Thus, the eigenvalues are $J_{11} < 0$ and J_{22} , and hence the stability is determined by the sign of the latter. Now, J_{22} is

$$J_{22} = s^2 \left(a_0 \left(\frac{u}{\sigma^2} \right)^2 e^{-1/2(u/\sigma)^2} - \frac{a_0}{\sigma^2} e^{-1/2(u/\sigma)^2} - d_1 f''(u) N \right), \quad (\text{A14})$$

which, by Equation (A5), can be reduced to

$$J_{22} = \frac{s^2 a_0}{\sigma^2} e^{-1/2(u^*/\sigma)^2} \left(u^* \left(\frac{f''(u^*)}{f'(u^*)} + \frac{u^*}{\sigma^2} \right) - 1 \right) \quad (\text{A15})$$

at equilibrium. Given Equations (A6) and (A10), we have

$$\frac{f''(u^*)}{f'(u^*)} + \frac{u^*}{\sigma^2} = \frac{f''(u^*)}{f'(u^*)} - H(u^*) < 0 \quad (\text{A16})$$

and so $J_{22} < 0$. Thus, both eigenvalues are negative, and the equilibrium is therefore stable. ■

Appendix 2

We obtained a suite of $2^7 = 128$ alternative logistic regression models by taking all possible combinations of the seven factors. When a factor was removed, every interaction term involving that factor also was removed. Each factor appeared in exactly 64 models. Each of the alternative models was fitted to the data using the method of maximum likelihood (ML), adjusted for overdispersion by a variance inflation factor [2, p. 68].

The Akaike weight w_k for the k th model in a set of R models, is given by

$$w_k = \frac{\exp(-(1/2)\Delta\text{AIC}_k)}{\sum_{i=1}^R \exp(-(1/2)\Delta\text{AIC}_i)} \quad (\text{A17})$$

and the factors are ranked in relative importance by the weighted sums

$$w_+(k) = \sum_{i=1}^R w_i I_{ki}, \quad (\text{A18})$$

where $I_{ki} = 1$, if variable x_k is in model i , and $I_{ki} = 0$ otherwise. Variables with higher values of w_+ are more important. We ranked the variables according to relative importance within each stage ($R = 64$) and also over all the stages (including STAGE as a seventh variable) and all the models ($R = 128$).

For nested regression models, there is often not a ‘clearly best’ model. That is, the model with $\Delta\text{AIC} = 0$ can vary from data set to data set under the same sampling conditions. Thus, parameter estimates should be based on all of the models to provide more stable inference [2]. The model averaged estimate for parameter β_k is

$$\hat{\beta}_k = \frac{\sum_{i=1}^{128} w_i I_{ki} \hat{\beta}_k^{(i)}}{w_+(k)}, \quad (\text{A19})$$

where $\hat{\beta}_k^{(i)}$ is the ML estimator of β_k in model i , and w_i is the Akaike weight for model i relative to all 128 models [2, p. 152]. Model-averaged estimates for sampling correlations between parameters, as well as the unconditional sampling variance and covariance, are computed as in Burnham and Anderson [2, pp. 162–163]. We wrote programs in MATLAB® for the analysis calculations, using the generalized linear model fitting function ‘glmfit’ in the Statistics Toolbox.

Descriptive statistics for the environmental correlates appear in Table A1. Mean relative humidity decreased and mean ambient temperature increased over the three stages of the breeding season. Wind speed was markedly lower during the incubation/chick-rearing stage than during the earlier two stages. Differences in mean solar elevation, tide height, and barometric pressure showed no clear trends.

Table A1. Descriptive statistics for environmental correlates.

| Factor | Mean | SD | Range | Min | Max |
|--|-------|-------|-------|--------|------|
| Nest-building/egg-laying stage ($J = 840$) | | | | | |
| HUM | 87.7 | 5.91 | 27 | 70 | 97 |
| TEMP | 12.0 | 1.28 | 6.6 | 9.3 | 15.9 |
| SUN | 34.5 | 20.7 | 65.7 | -2.17 | 63.5 |
| WIND | 1.52 | 1.57 | 8 | 0 | 8 |
| TIDE | 1.09 | 0.866 | 3.30 | -0.671 | 2.63 |
| BAR | 759 | 4.33 | 16.8 | 750 | 767 |
| Egg-laying/incubation stage ($J = 799$) | | | | | |
| HUM | 78.8 | 9.23 | 45 | 51 | 96 |
| TEMP | 14.1 | 1.52 | 9.4 | 10.7 | 20.1 |
| SUN | 35.9 | 20.8 | 63.9 | 1.24 | 65.2 |
| WIND | 1.75 | 0.964 | 4 | 0 | 4 |
| TIDE | 1.02 | 0.867 | 3.38 | -0.776 | 2.60 |
| BAR | 766 | 3.78 | 12.1 | 760 | 772 |
| Incubation/chick-rearing stage ($J = 753$) | | | | | |
| HUM | 71.8 | 22.2 | 73 | 25 | 98 |
| TEMP | 18.7 | 5.00 | 20.2 | 12.2 | 32.4 |
| SUN | 34.8 | 20.7 | 63.8 | 0.23 | 64.0 |
| WIND | 0.790 | 0.896 | 3.1 | 0 | 3.1 |
| TIDE | 1.17 | 1.01 | 3.29 | -0.784 | 2.51 |
| BAR | 760 | 2.13 | 8.5 | 756 | 765 |

Notes: J is the number of scans, HUM is the relative humidity as a percent, TEMP is the temperature in degree Celsius, SUN is the solar elevation measured as degrees above the horizon, WIND is the wind speed on the colony in m/s, TIDE is the tide height in m, BAR is the barometric pressure in mmHg.