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**BREEDING SNOWY PLOVERS (*Charadrius alexandrinus*) EXHIBIT VARIABLE
RESPONSE TO HUMAN DISTURBANCE ON TWO ISLANDS IN SOUTHWEST
FLORIDA**

By

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A thesis submitted to the Graduate School-New Brunswick

Rutgers, The State University of New Jersey

in partial fulfillment of the requirements for the degree of

Master of Science

Graduate Program in Ecology and Evolution

written under the direction of Dr. David Ehrenfeld

and approved by

New Brunswick, New Jersey

October 2010

ABSTRACT OF THE THESIS

Breeding Snowy Plovers (*Charadrius alexandrinus*) exhibit variable response to human disturbance on two islands in southwest Florida

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Human disturbance has been implicated in population declines and decreased productivity in shorebirds, including the Snowy Plover, around the world. In this study, we examined the response of Snowy Plovers nesting on two islands in southwest Florida, Sanibel and La Costa Islands, to human disturbance. We recorded flush distances and time spent off the nest for incubating birds in response to approach by a human on both Sanibel and La Costa, and for approach by a leashed dog on Sanibel only. We also

recorded the first reaction distance of Snowy Plover adults and broods to approach by a human on both islands, and activity budgets of adults and chicks in the presence and absence of human activity. We conducted Bayesian analyses on all approach data. We used Principal Component Analysis, followed by Multivariate Analyses of Variance on activity budget data to examine the effect of people on bird behavior. We found that incubating birds on Sanibel flushed at significantly shorter distances from a person than did birds on La Costa; additionally, we found that Sanibel birds flushed at significantly greater distances from a dog than from a person. For time off nest, we found that birds remained off a nest for a significantly longer period of time following a flush by a dog than by a person; no difference between birds nesting on Sanibel and La Costa, however, was observed for time off nest. Brood reaction distance remained constant over the pre-fledged period and did not differ between broods that fledged and those that did not. We found that broods from La Costa reacted to human disturbance at greater distances than did broods on Sanibel. Additionally, human presence, regardless of activity type, resulted in altered behavior of Sanibel Snowy Plovers. In particular, running and foraging behaviors decreased, while walking increased. Beach driving vehicles also resulted in altered behavior of Sanibel Island broods. The presence of vehicles resulted in increased sitting and decreased standing.

Acknowledgments

I thank the Sanibel-Captiva Conservation Foundation, the Sanibel-Captiva Audubon Society, and J.N. “Ding” Darling National Wildlife Refuge for project funding, Sanibel-Captiva Conservation Foundation staff and volunteers for assistance with monitoring and data collection, my graduate committee for guidance, and finally The Clarks for use of their Golden Retriever as “Plover Dog.”

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Chapter 1

Abstract

Snowy Plovers (*Charadrius alexandrinus*) are believed to be threatened by human disturbance across their range. In this study, we examined the response of Snowy Plovers incubating nests on two islands in southwest Florida to human disturbance. We recorded flush distances and time spent off the nest following disturbance by a single person for Snowy Plovers on Sanibel and La Costa Islands, and by a person walking a dog on Sanibel only. Using the Bayesian analyses run in the program WinBugs, we determined that birds nesting on Sanibel flushed at statistically significantly shorter distances from a solitary person than the birds nesting on La Costa. For the time spent off a nest following a flush by a single person, there was no difference between birds nesting on Sanibel and La Costa islands. On Sanibel, nesting birds also flushed at statistically significantly greater distances and spent statistically significantly more time off a nest when flushed by a person walking a dog than by a person alone. These results indicate that nesting Snowy Plovers show a variable response to human disturbance that may result from the birds' typical exposure levels to human disturbance.

Introduction

The Snowy Plover (*Charadrius alexandrinus*) is a small shorebird that nests in several metapopulations on beaches and mud and salt flats across the United States. In the United States, the Western Snowy Plover is currently listed as threatened under the Endangered Species Act, and several states, including Florida, have also listed the species as state threatened (Page et al. 1995). Snowy Plovers typically prefer areas that are sparsely vegetated as nesting sites (Page et al. 1985, Smith 2008). In Florida, Snowy Plovers nest on sand beaches in two metapopulations, with limited dispersal recorded between the Florida panhandle population and the southwest Florida population (B. Smith, pers. com.). Florida Snowy Plovers nest from mid-February until mid-August, and may nest up to three times, depending on nesting success early in the season (Himes et al. 2006, Amat et al. 1999). Color banding efforts on Sanibel and La Costa islands suggest that the population in southwest Florida includes females that may remain with a given male throughout a season or may breed with multiple males in a season (SCCF, unpublished data). The typical brood size for the Snowy Plover is three chicks per nesting attempt; chicks are precocial and are guarded by one or both parents at least until fledging.

Gill et al. (2001) have suggested that research and conservation efforts be concentrated on threatened species or species for which human disturbance has been implicated in population declines. The Snowy Plover, like many shorebird species, is currently faced with an array of threats that are thought to limit nesting success in the United States;

habitat loss and human disturbance within nesting habitat have been suggested as major contributing factors to declining shorebird populations through deleterious effects on breeding success (Himes et al. 2006, Ruhlen et al 2003). In Florida, available beaches range in human disturbance from remote beaches characterized by low human visitation, to resort beaches where the number of people utilizing the beach may total hundreds per day. Himes et al. (2006) estimate that 68% of Florida sites containing suitable nesting habitat are characterized by high levels of human disturbance. Recent research points to negative effects of human disturbance on incubating shorebirds leading to decreased productivity resulting from trampling, increased absences from nests, and possibly thermal stress (Schulz and Stock 1993, Weston and Elgar 2005, and Yasué and Dearden 2006). Rodgers and Smith (1995) have shown that colonial shorebirds flush from nests due to human disturbance in a manner correlated both with species and with approach type; they did not include any data on solitary nesting species, such as the Snowy Plover, nor did they include flush distances from a person walking a dog. Byrkjedal (1989) examined defensive behavior of flushed incubating Lesser Golden Plovers in Manitoba, Canada, where the birds' exposure to people was low, and noted that behavioral response patterns to people and dogs were similar.

In this study, we attempted to determine the range of distances at which incubating Snowy Plovers flushed from either a solitary human or a human walking a leashed dog. Currently, dogs are allowed on most nesting beaches of the Snowy Plover in Florida. Guidelines for staking set-back distances for nesting shorebirds in Florida, following the

suggestions of Rodgers and Smith (1995), are at distances only meant to prevent disturbance by humans and boats, not disturbance by humans with dogs.

Methods

The study area contained two islands in southwest Florida, Sanibel Island and La Costa Island; both islands are barrier islands located on the Gulf of Mexico known to support Snowy Plover nesting in recent years with sparsely vegetated sand and shell beaches. Sanibel is a resort island accessible by car, with ten miles of beaches that are characterized by high levels of disturbance by humans, dogs, and vehicles. The remote La Costa Island is accessible only by boat, and disturbance by humans, dogs, and vehicles is typically low. Both islands currently maintain natural beaches, i.e. they neither rake nor groom the beaches.

During the breeding seasons of 2008 and 2009, from the beginning of March through mid August, with the help of seven field assistants and nine volunteers, we monitored adult Snowy Plovers with no more than three days between observations until nesting was observed. Once a nest was located, we staked it at a distance great enough from the nest to prevent flushing by the bird when a person (or persons) approached the staking. For each nest, we determined or estimated a full clutch date (when egg-laying was thought to be complete) using the methods of Hood (2006), and estimated a hatch date by counting 28 calendar days from the full clutch date. We monitored incubating nests with no more than 3 days between observations, and checked nests every day (Sanibel) or every other day (La Costa) starting at approximately the 23rd day of incubation to ensure that we accurately recorded the final status of the nest (eggs hatched or nest failed).

Because the Snowy Plover is a state-listed species in Florida, before starting data collection in 2008, we obtained Florida Fish and Wildlife Conservation Commission (FWCC) permit #WX08219 to legally flush incubating Snowy Plovers from April 25, 2008 until December 31, 2009. During the period of nest incubation, a single researcher approached each incubating nest on both islands once per week (for a maximum of four observations per nest) to determine the flush distance from a human, as well as the time spent off the nest following disturbance. Douglas et al. (2009) reported that nesting mockingbirds learn to identify human intruders and vary their behavioral responses accordingly. To minimize acclimatization to a specific human over the course of the two nesting seasons, a total of eight researchers of both sexes, with varied appearances (i.e. varied clothing) from day to day were involved in the study, and we limited approaches to once per week per nest. We placed large shells (collected from Sanibel and La Costa islands) with a spray-painted yellow spot at 2.5 m intervals from the nest to the outer edge of the staking in order to closely estimate the distance at which the flush occurred. During the 2008 season, much of the nesting on La Costa occurred within a large area previously staked by the Florida FWCC for nesting shorebirds (including Least Terns, Snowy Plovers, Wilson's Plovers, and American Oystercatchers), necessitating an alteration in the methods for approaches to incubating birds. For these nests, shells marking distance were not feasible due to the arrangement of the staking, so we marked a line in the sand at the distance where flushing occurred, and then measured the flush distance on a plane parallel to the nest.

We always approached nests at a slow walk (approximately 0.75 meters per second) directly from the surf towards the nest after verifying that no other potential disturbances (people, dogs, predatory birds, etc.) were present and that the incubating bird appeared undisturbed. As soon as the bird flushed, the researcher noted the distance from the nest and the time, then quickly walked away. A second researcher observed from a distance outside the flush range to determine the time spent off the nest. We also recorded data on the environmental conditions at the time of the approach, as well as the sex of the bird (if known).

On Sanibel, in addition to collecting data on flush distances from a human, we also recorded flush distances from a person walking a leashed dog. We did not collect this data on La Costa because dogs are prohibited on the beaches in Cayo Costa State Park, where Snowy Plover nesting occurred. For approaches made with a leashed and muzzled dog, one person walked the dog and another observed the incubating bird with binoculars without disturbing the bird and causing a flush. The dog-walker began an approach from a distance outside the flush range (around 150 m) and walked towards the nest at the edge of the water, parallel to the surf. The dog-walker made a line in the sand when the flush occurred, and immediately turned and walked the dog outside of the flush range again. The observer recorded the time spent off the nest by the incubating bird and then measured from the mark to the edge of the staking. We recorded distances from the nest

to the staking after the nest was no longer active to minimize additional disturbance and then added those distances together to calculate the flush distance.

Statistical Analyses

Frequentist statistical methods typically require that certain basic assumptions be met that are often violated in behavioral ecology datasets (Garamszegi et al. 2009). Behavioral research is routinely limited by both small sample size and missing data, making the Bayesian framework ideal for analyses of these datasets; Bayesian statistical inference enables scientists to draw meaningful conclusions from analyses even with small sample size and missing values (Ellison 1996, Garamszegi et al. 2009). The major frequentist objection to Bayesian inference is the use of prior knowledge in the assignment of prior probability distributions; this is easily avoided, however, by assigning “vague priors”. Vague priors are relatively flat probability distributions that assume no prior knowledge of the system, such that posterior probability distributions of parameters result from the data rather than prior knowledge (Brooks 2003). When vague priors are used, comparable Bayesian and frequentist methods generally produced similar results (Garamszegi et al. 2009).

We conducted two Bayesian analyses using the statistics program WinBUGS version 14.3 (Lunn et al. 2000) to compare the mean flush distances and time spent off the nest for flushes from a human on both Sanibel and La Costa, as well as a human with a dog on

Sanibel. We deemed a Bayesian hierarchical model framework appropriate for this dataset in order to account for the hierarchical, unbalanced, repeated measures study design. We analyzed flush distance and time off nest separately first in a “full model” as functions of the three groups (Sanibel-human, Sanibel-dog, La Costa-human), and second in a “reduced model” to determine the importance of the groups. The full model included island and approach type (modeled as the group) as biologically significant variables, while the reduced model eliminated island and approach type variables and assumed that all data were drawn from one group instead of three. We used Deviance Information Criterion (DIC) to compare models and selected the model with lower DIC (Spiegelhalter et al. 2000). Prior to conducting analyses, we assessed both datasets for normality using normal probability plots and subsequently natural log-transformed the data to normalize it. We reconverted distance data to meters and time data to seconds for reporting purposes.

In order to compare the means between groups, we chose a Bayesian model framework loosely analogous to the frequentist Repeated Measures Analysis of Variance (ANOVA). Additionally, instead of assuming a constant population variance, by using a Bayesian framework, we could allow for different variances between groups. To show little prior knowledge about the study parameters, we assigned vague prior and hyperprior probability distributions (prior probability distribution of a prior probability distribution) in all cases.

The datasets for both flush distances and time off nest, $\log(Y_i)$, were considered to be drawn from a normal distribution with a mean μ for each group, variable i , and nest, variable j , and precision τ (the inverse of the variance). We show the full model with all parameters, priors, and hyperpriors in Table 1. We followed the recommendations of Lunn et al. (2000) for the selection of all vague prior and hyperprior distributions and parameters.

In the reduced model, the datasets were considered to be drawn from a single group i with mean θ . The data level equation (Table 1) remained the same in the reduced model. Theta, however, was said to be drawn from normal distribution with parameters mean equal to 0, and precision equal to 1.0E-10 (Equation 1).

$$\theta_i \sim \text{Normal}(0.0, 1.0E-10) \quad \text{Equation 1}$$

Prior distributions for τ and η were vague, remaining the same as those in Table 1.

Model simulations were run in WinBUGS 14.3 until parameter convergence was achieved (20,000 iterations). Posterior mean estimates of parameters were then determined from a further 50,000 iterations.

Results

We located and staked twenty-five nests to prevent human disturbance during the 2008 and 2009 nesting seasons on Sanibel. Of these, eggs from nineteen nests hatched successfully. On La Costa Island, we located twenty-three nests over both field seasons and eggs from eight of these hatched. We used thirty of these forty-eight nests, eleven from La Costa and nineteen from Sanibel, in these analyses. We did not include nests in analyses if either the eggs hatched before data collection for the study began in 2008, or they failed to hatch before data on incubation could be collected.

We also recorded staking distances around nests when possible; the distances that we recorded included the distance from the front of the staking (towards the Gulf) to the nest, the distance from the left side staking to the nest (left side when facing the dune vegetation), and the distance from the right side staking to the nest (right side when facing the dune vegetation). On Sanibel, the average staking distances were 8.0 m to the front, 9.0 m to the left side, and 8.2 m to the right side. On La Costa, the average staking distances were 29.0 m to the front, 18.6 m to the left side, and 19.2 m to the right side.

Model Selection

We compared DIC between the full model and the reduced model for both datasets and selected the model with lower DIC. For the flush distance dataset, the full

model resulted in a DIC of 797.50 while the reduced model resulted in a DIC of 1017.50. We therefore selected the full model, incorporating different groups, as a better fit to the data.

We also selected the full model for the time off nest, with a lower DIC than the reduced model, as the better fit to the data. The DIC value for the full model is 473.76, while the reduced model resulted in a DIC value of 517.76.

Parameter Estimates

Flush Distance

When the natural log-transformed results are converted to results in meters, the credible interval for the Sanibel-human group is from 3.3 m to 5.5 m with a mean distance equal to 4.3 m, the credible interval for the Sanibel-dog group is from 17.0 m to 29.6 m with a mean equal to 22.6, and the credible interval for the La Costa-human group is from 13.1 m to 26.7 m with mean equal to 19.0 m. The results of the simulation indicate that there is a statistically significant difference between the Sanibel-human and Sanibel-dog groups, as well as between the Sanibel-human and La Costa-human groups (Figure 1). There is no significant difference between the Sanibel-dog group and the La Costa-human group.

Time Off Nest

In seconds, the credible interval for the Sanibel-human group is 23 s to 46 s, with a mean of 33 s. For the Sanibel-dog group, the credible interval is from 76 s to 153 s, with a mean of 110 s. The credible interval for the La Costa-human group is from 18 s to 46 s, with a mean of 29 s. There is no significant difference between the time spent off nest for the Sanibel-human and the La Costa-human groups (Figure 2). There is, however, a significant difference between the Sanibel-human and Sanibel-dog groups, as well as the La Costa-human and Sanibel-dog groups.

Discussion

Analysis of the data shows that, on Sanibel, there is a distinct difference in the distance at which Snowy Plovers flush from approach by a solitary human versus a human walking a leashed dog. The average distance at which a bird first flushes from a leashed dog (22.6 m) is more than five times greater than the average distance at which a bird flushes from a human (4.3 m). Additionally, birds flushed by approaching dogs spent longer periods of time away from a nest than did birds flushed by a person alone. In fact, the average time spent off the nest by Sanibel birds flushed by a dog (109 s) is more than three times the length of time spent off the nest when flushed by a solitary person (33 s).

From the results of this analysis, it is clear that the distances used for symbolic staking on Sanibel, aimed to prevent disturbance by human activity on the beach, while sufficient to prevent disturbance from approach by a human, is insufficient to prevent disturbance by leashed dogs walked on the beach. Staking on Sanibel will need to be at a distance greater than ~ 30 meters in order to exceed the Bayesian credible interval for flush distances from a dog and minimize disturbance by dogs to nesting Snowy Plovers.

Although it is impossible to definitely determine the cause of the difference in flush distance from a human between Sanibel and La Costa islands because the data are confounded, we conjecture that the difference in flush distances may result from the vast

difference in visitation and management on the two islands. Sanibel is heavily visited and densely populated compared to La Costa. This possible explanation is intriguing from a managerial standpoint because the Snowy Plover may have a greater adaptability to human disturbance than previously expected. Previous work on the effects of human disturbance on the nesting success of Snowy Plovers has not included breeding sites as consistently and heavily visited as Sanibel. Many heavily visited beaches are often intensely managed by beach raking, making them unsuitable for shorebird nesting. It may be that historic nesting sites for Snowy Plovers that have been assumed to be abandoned due to generic human disturbance, actually only require a single managerial change, such as the cessation of beach grooming, to become reestablished as productive nesting beaches. This possibility warrants further study at other breeding sites for the Snowy Plover.

It is interesting to note that, while the birds on La Costa Island flush at a larger distance from approach by a person than on Sanibel Island, they do not spend a greater amount of time off the nest following a flush event. This result additionally suggests that these birds have a greater tolerance of human presence during the nesting season than previously supposed.

Higher tolerance for human activity may very well imply a much improved outlook for the future of this species. Further research expanding upon the results of this study is

essential to determine whether Snowy Plovers nesting on beaches heavily visited by people do in fact show an increased tolerance for human disturbance as compared to those nesting on relatively low traffic beaches. If this proves to be the case, research will need to identify which aspects of many high traffic beaches are actually contributing to the abandonment of nesting at historic sites. Once identified, new management must be implemented to reflect improved understanding of the requirements for nesting by Snowy Plovers and other solitary beach nesting bird species.

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Tables and Figures

Table 1. Full Bayesian hierarchical model for flush distance and time off nest. Vague prior and hyperprior distributions were assigned to δ , τ , η , and ϕ .

	Model	Parameters
Data level	$\log(Y_i) \sim$ Normal distribution	Mean μ (group i, nest j), precision τ
	$\tau \sim$ Gamma distribution	Mean 0.001, precision 0.001
	$\mu_i \sim$ Normal distribution	Mean θ , precision η
	$\eta \sim 1/\sigma^2, \sigma^2 \sim$ Uniform distribution	Mean 0, precision 200
	$\theta_i \sim$ Normal distribution	Mean δ , precision ϕ
	$\phi \sim 1/\sigma^2, \sigma^2 \sim$ Uniform distribution	Mean 0, precision 200
	$\delta \sim$ Normal distribution	Mean 0, precision 1

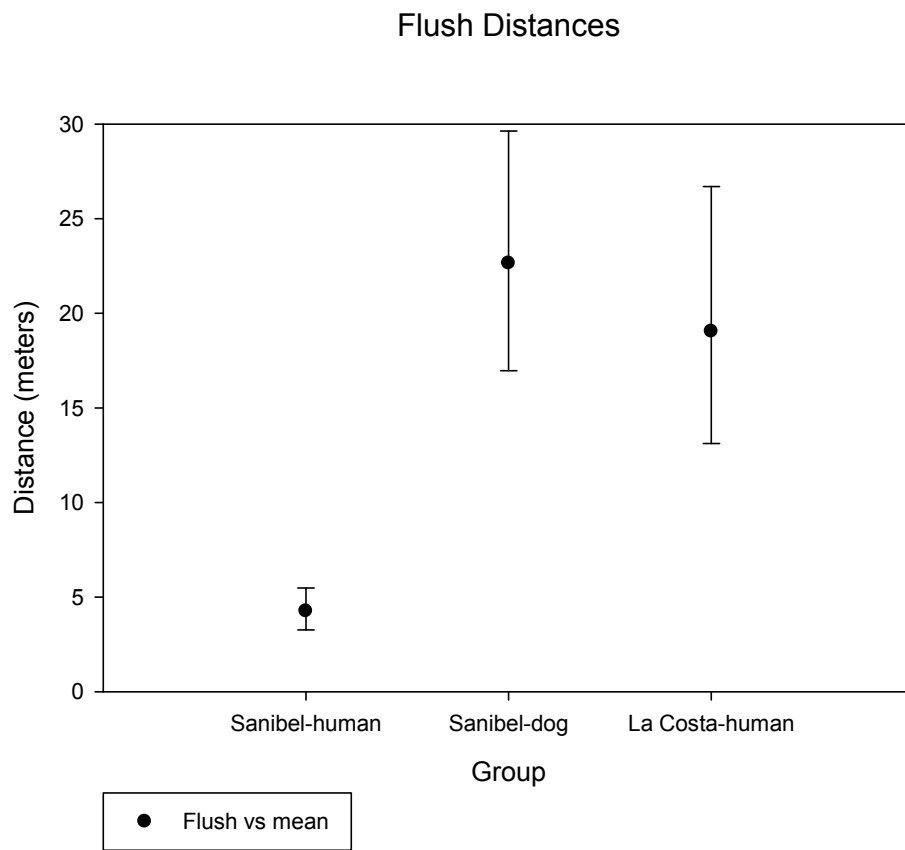


Figure 1. Flush distances of incubating Sanibel and La Costa birds following a flush by a human or dog on Sanibel and a human on La Costa.

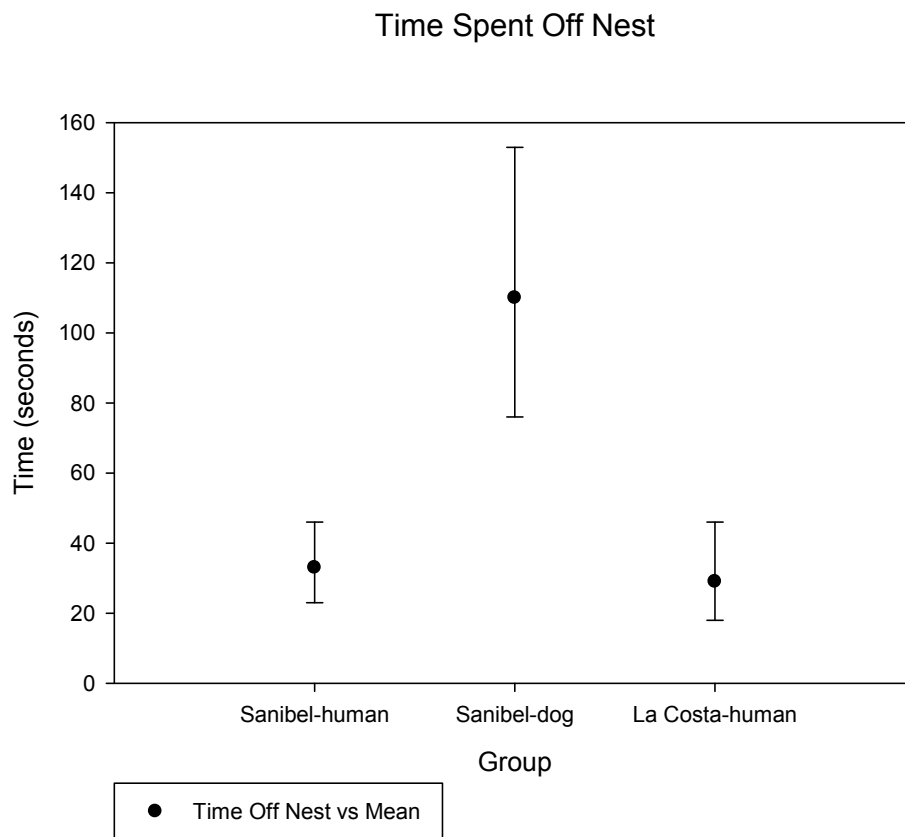


Figure 2. Time spent off a nest by incubating Sanibel and La Costa birds following a flush by a human or dog on Sanibel and a human on La Costa.

Chapter 2

Abstract

Human disturbance has been implicated in decreased survival rates of Snowy Plover (*Charadrius alexandrinus*) broods, but little is known about their direct reactions to human presence. In this study, we compared the distance at which broods on two islands in southwest Florida, Sanibel and La Costa Islands, first reacted to approach by a human. We also created activity budgets for both adults and chicks in the presence and absence of various types of human disturbance (dog-walking, running, sitting, standing, driving a vehicle on the beach, and walking) to examine the effects of human activities on bird behaviors. Using Bayesian analyses run in the program WinBUGS, we determined that there is no change in brood reaction distance over time and no difference in reaction distance between broods that survived to fledge and those that did not survive to fledge. Broods reared on Sanibel Island reacted to human disturbance at a statistically significantly shorter distance than did broods reared on La Costa Island. We found that human presence significantly affects the behavior of Snowy Plovers on Sanibel by decreasing foraging and running behaviors but increasing walking. Additionally, beach-driving vehicles result in significantly higher levels of sitting behavior and significantly lower levels of standing behavior in Sanibel chicks. Sample sizes were too small to calculate if the behavior of La Costa Island birds is affected by human presence. As Snowy Plovers can nest successfully on developed beaches, management strategies must be tailored to encourage recolonization of historic nesting locations and to improve nesting success of Snowy Plovers on developed beaches within their historic range.

Introduction

Human disturbance has been implicated in altered foraging behaviors of Piping Plovers (*Charadrius melodus*) and in reduced chick survival in the Snowy Plover (*Charadrius alexandrinus*). Goldin and Regosin (1998) reported that Piping Plover chicks on beachfront habitats spent as much 17% of observed time responding to human disturbance. Piping Plover broods in Nova Scotia exposed to increased human disturbance spent less time foraging and being brooded, and had lower survival rates than broods that experienced less frequent disturbance (Flemming et al. 1998). The beaches in Nova Scotia can be categorized as very low disturbance beaches at the time of the study (0 to >20 visits per week). Ruhlen et al. (2003) similarly reported increased mortality rates of Snowy Plovers in California on weekends compared to weekdays, and attributed the difference to increased beach visitation by recreational users on weekends, but they did not categorize the general level of disturbance in their study site. Weston and Elgar (2005) compared chick behavior in Hooded Plovers (*Thinornis rubricollis*) on low disturbance days, in which chicks experienced a mean of 45.2 encounters with humans, to high disturbance days, in which broods experience a mean of 83.9 encounters; their results suggest that chick brooding and foraging decreased with higher levels of disturbance. Although human disturbance has been implicated in chick mortality in shorebirds, including the Snowy Plover, researchers have yet to determine how human disturbance is altering chick behavior in Snowy Plovers.

Results of research and monitoring on Sanibel Island, Florida, have seemed to contradict the conclusions from the above mentioned studies. On Sanibel Island, Snowy Plovers have historically nested on two stretches of beach, the west end and the east end. The east end of the island is characterized by heavier human beach traffic and narrower beaches, while the west end is characterized by lower beach traffic and typically wider beaches. Smith (2008) reported the interesting result that fledging success was actually 2.7 times greater on the more heavily trafficked east end of Sanibel than on the west end from 2002 to 2005. Starting with the 2006 nesting season, Snowy Plover nesting on the west end ceased entirely.

On Sanibel Island, where Snowy Plover broods routinely encounter > 50 people in a fifteen minute period (SCCF, unpublished data), nesting success remains fairly high on the east end of the island. During the monitoring period on Sanibel from 2002-2009, an average of 31.5% of hatched chicks survived to fledge (approximated as survival to day thirty when actual flight was not observed), with the highest annual rate equaling 66.7% of hatched chicks surviving to fledge in 2007 (SCCF, unpublished data).

Gill et al. (2001) have noted that research is needed to better understand the relationship between fitness and behavioral changes in the presence of disturbance. In order to analyze the effects of human disturbance on Snowy Plovers on Sanibel and La Costa Islands, we conducted a two-part study, in which we attempted to quantify the distance at

which Snowy Plover broods first reacted to human disturbance on both islands, as well as to determine what changes in behavior, if any, occurred in the immediate vicinity of human disturbance.

Methods

During the breeding seasons of 2008 and 2009, eight researchers and nine volunteers located and staked-off Snowy Plover nests to minimize human disturbance on the islands of Sanibel and La Costa in southwest Florida. Once a nest hatched, we monitored broods most days until we determined brood fate. The maximum time between brood checks was two days. We recorded broods as fledged if they survived at least thirty days after hatching or if chicks were seen flying. Due to the small number of broods on either island at any given time and the frequency of monitoring, we identified broods by location, chick size and any unique identifiers of adults (examples include unusual plumage, bands, or a missing foot). Additionally, in 2009 we banded adult nesting birds with unique color-band combinations to further aid in brood monitoring.

We collected data under Florida Fish and Wildlife Conservation Commission (FWCC) Permit # WX08291 to determine the distance at which chicks and adults with chicks first reacted to an approach by a human on Sanibel and La Costa Islands during the 2008 and 2009 nesting seasons. Researchers included three men and five women. A single researcher approached a chick (or chicks) only after the behavior of the chick and any adults present was verified as undisturbed, and after the researcher had confirmed that no other potential disturbances were present. The researcher then approached a chick at a slow walk (0.75 m per second) and marked a line in the sand at both the location of first disturbance and the location of the chick at first disturbance. The distance was then measured between the two lines. The direction of the approach was variable, and

depended on the observer's ability to confirm that the chick's or adult's change in behavior indeed resulted from the approach. We considered several behaviors to be disturbance behaviors, and first reaction could occur by an adult, a chick, or both; behaviors included vocalization, vigilance, suddenly standing, running or walking away. We also collected data on the environmental conditions at the time of the approach. We approached each brood four times per week, no more than once per day, for a total of 17 possible observations prior to fledging at 30 days.

Activity budgets can be used to quantify bird behavior (Morrier and McNeil 1991). We created activity budgets for adult birds and chicks in the presence and absence of human disturbance to determine whether human activity significantly alters behavior of chicks and adults. We observed individual adults and broods a maximum of two times per day, morning and afternoon. First we located an adult or chick for observation and identified its nest number if possible. The researcher observed the bird from a distance greater than twenty meters using binoculars for seven minutes, while recording its behavior every twenty seconds and the number and activities of people within ten and twenty meters using an interval timer. Bird behavior categories included antipredator (running and "broken-wing" display for adults, running, sitting motionless in sand or vegetation for chicks), flying, foraging, preening, running, sitting, standing, and walking. Human activity categories included dog-walking, running, sitting, standing, driving a motorized vehicle, or walking. If the observation was discontinued with less than five minutes of data, the researcher started over to collect a minimum of five minutes of data. If the bird

approached the researcher, the researcher held his position, but never included himself when counting the number of people in the bird's vicinity. When the bird moved a distance greater than forty meters away from its starting position, the observation was discontinued. We also recorded environmental conditions for each observation.

In order to standardize the researchers' ability to estimate the distances of people from the bird, we practiced estimating distances first with a "dummy plover" (a piece of white PVC pipe close in size to an adult plover) and small flags and later by conducting practice observations on birds. When a researcher was unsure into which category to place an individual during an observation, the protocol dictated that the person be included within the lower category. Thus, if the researcher was unsure whether an individual walking past a bird was within 10 meters or just outside 10 meters, the individual was recorded as within 10 meters.

Statistical Analyses

Behavioral ecology datasets often violate certain basic assumptions required for the application of frequentist statistical methods (Garamszegi et al. 2009). They are often limited by both small sample size and missing data; the Bayesian framework is therefore ideal for analyses on these datasets since it enables scientists to draw meaningful conclusions from analyses even with small sample size and missing values (Ellison 1996, Garamszegi et al. 2009). By assigning "vague priors" (relatively flat probability

distributions that assume no prior knowledge of the system), Bayesians can avoid the major frequentist objection to Bayesian inference because the posterior probability distributions of parameters are informed from the data rather than from prior knowledge (Brooks 2003). Frequentist and Bayesian methods generally produced similar results when vague priors are used (Garamszegi et al. 2009).

For brood reaction distances to human disturbance, we conducted Bayesian analyses to determine whether reaction distance was influenced by brood age, fledging success, and island. Douglas et al. (2009) reported that mockingbirds can learn to recognize individual humans; we deemed it possible, therefore, that reaction distance could be affected by brood age because adults and chicks might become acclimated to human disturbance in general or to the researchers in particular over the course of the thirty day pre-fledged period. We also thought it reasonable that as chicks become more independent and forage at greater distances from adults, parental vigilance might decrease. Furthermore, if human disturbance does indeed influence chick survival, reaction distances between broods that survived to fledge, compared with those that did not, could be different as well. We assessed reaction distance data for normality using normal probability plots and natural log-transformed the data to achieve normality.

To determine if reaction distance changed over the thirty day period prior to fledging, we assumed reaction distances of each brood to be correlated and to follow a multivariate-

normal distribution with population mean vector μ and precision (inverse of the variance) matrix Ω . To determine the relationship of the reaction distance measurements over time (constant distance over time, linear growth curve, or quadratic growth curve), we fitted three equations to the data to model μ . To demonstrate little prior knowledge about the parameters, we assigned vague prior and hyperprior probability distributions (prior probability distributions of prior probability distributions) in all cases. We show the full model with all parameters, priors, and hyperpriors in Table 2. We followed the recommendations of Lunn et al. (2000) for the selection of all vague prior and hyperprior distributions and parameters.

Model simulations were run in WinBUGS 14.3 (Lunn et al. 2000) until they converged (50,000 iterations) and then we determined posterior mean estimates of parameters from an additional 50,000 iterations. We used the credible interval for β_1 to select the model of constant distance as the best fit, due to the fact that the credible interval of β_1 included zero (Table 3); this indicates that zero is a realistic value for the change in reaction distance over time.

Once we selected the constant distance equation as the best fit to the data, we treated the data as simple repeated measures in analyses to assess the effect of brood survival and island on reaction distance. We used a Bayesian model framework analogous to a frequentist Repeated Measures Analysis of Variance (ANOVA) in all subsequent

analyses on brood reaction distance as the “full model”. The full model included either island or brood survival (modeled as the group) as the biologically significant variable, while the reduced model eliminated the island and brood survival variable and assumed that all data were drawn from one group instead of two. To measure the effect of brood survival (data only from Sanibel) or island on reaction distance, $\log(Y_i)$ was considered to be drawn from a normal distribution with a mean μ for each group i (i.e. Failed or Fledged and Sanibel or La Costa) and nest j and precision τ (inverse of variance). We show the full model with all parameters, priors, and hyperpriors in Table 3. We again followed the recommendations of Lunn et al. (2000) for the selection of all vague prior and hyperprior distributions and parameters.

Datasets in the “reduced model” were considered to be drawn from a single group i with mean θ . The data level equation remained the same (Table 3), but θ was said to be drawn from normal distribution with parameters mean equal to 0.0, and precision equal to 1.0E-10 (Equation 2).

$$\theta_i \sim \text{Normal}(0.0, 1.0\text{E}-10)$$

Equation 2

Prior distributions on τ and η were vague, remaining the same as those in Table 3.

We again used WinBUGS 14.3 to run model simulations until parameters converged (20,000 iterations). We used a further 50,000 iterations to estimate posterior means of parameters. In these analyses we selected the model (“full” or “reduced”) with lower DIC as the better fit to the data (Spiegelhalter et al. 2000).

Principal Component Analysis (PCA) and Multivariate Analysis of Variance (MANOVA) are both straightforward using frequentist techniques (McGarigal et al. 2000) compared to analogous analyses using Bayesian methods. For this reason we judged it most appropriate to use frequentist techniques for the analyses on the activity budget dataset. We first conducted a PCA in SAS 9.2 using the PrinComp procedure to condense the number of response variables; we also removed the antipredator group at this time due to insufficient number of observations. As we had already performed the PCA using SAS 9.2, we deemed it simplest to analyze the PCA results also in SAS 9.2. Therefore, we conducted several MANOVAs using the GLM (generalized linear model) procedure with a MANOVA statement in SAS 9.2 on the reduced dataset to examine the effects of people on bird behavior; we examined the effects of several human activities in addition to simple presence or absence of humans, including dog-walking, running, sitting, standing, driving a vehicle, or walking. Then we further divided the dataset by island and bird age, to identify any differences in the birds’ reactions to people based on those variables.

Results

Over the course of the 2008 and 2009 field seasons, we located twenty-seven broods, nineteen from Sanibel Island and eight from La Costa Island, and monitored them for survival. Of these twenty-seven broods, we included twenty-three in these analyses. If a brood fledged before data collection began in 2008 or if it did not survive long enough for data to be collected, we did not include it in the analyses. None of the five broods that we included from La Costa survived past day five. Of the eighteen broods included from Sanibel, fourteen survived until fledged. The maximum number of days we observed a non-surviving Sanibel brood was twelve days. Additionally, we collected a total of 564 activity budgets, 116 of which were from La Costa Island and 448 of which were from Sanibel Island. Because human presence is uncommon on La Costa Island, we did not collect any activity budgets for adults in the presence of people dog-walking, running, or sitting. For chicks, we only collected activity budgets in the absence of people within twenty meters or in the presence of a vehicle. We only recorded bird age (adult or chick) and bird location (Sanibel or La Costa) for this study because it was frequently impossible to identify individual birds.

Model selection

To select the appropriate model for change in reaction distance over time, we examined the credible interval for β_1 (Table 4). Because the credible interval for the

parameter included the value zero, no change in reaction distance over time was indicated. For this reason we selected the constant reaction distance model.

After comparing DIC scores between the full and reduced models for island effect, we selected the full model. DIC for the full model was 391.72 and for the reduced model it was 401.54.

For brood survival, DIC proved to be inconclusive; DIC for the full model was 366.74 and DIC for the reduced model was 365.38. Credible intervals for θ from each group (failed vs. fledged broods) indicate that there is no difference for the two groups (Table 5).

Parameter Estimates

Change in Reaction Distance over Time

We report the results from the simulation for the change in reaction distance over time in Table 4. Since the interval includes zero, there was no change in brood reaction distance to human disturbance over time.

The Effect of Brood Survival on Reaction Distance

There was no significant difference in the posterior mean estimates for failed vs. fledged broods on Sanibel (Table 5). The credible interval for fledged nests is completely encompassed by that of the failed nests, showing that there is no significant difference in reaction distance to human disturbance between the two groups.

The Effect of Island on Reaction Distance

When natural log-transformed credible intervals are converted to meters, it is obvious that island affects the reaction distance of broods. On Sanibel, the credible interval for reaction distance is from 6.2 m to 7.4 m with a mean value of 6.7 m. The credible interval for brood reaction distance on La Costa is from 10.3 m to 18.0 m, with a mean value of 13.8 m. This result is statistically significant since there is no overlap between the credible intervals for the two groups.

The Effect of Human Presence on Behavior

To study correlations between behaviors examined in the activity budgets, we conducted a Principal Component Analysis (PCA) (N=448), resulting in a total of six axes. Principal component 1 (PC1) accounted for 41.1%, principal component 2 (PC2) for 28.5%, principal component 3 (PC3) for 13.2%, principal component 4 for 8.9%, principal component 5 for 7.4%, and principal component 6 for 0.9% of total variation. Because the first three principal components accounted for 82.8% of total variation, we used these in subsequent analyses. We show correlations of six behaviors to PC1, PC2, and PC3 in Figure 3.

We conducted multivariate analyses of variance (MANOVA) on PC1, PC2, and PC3 to examine the effects of the human activity in the birds' vicinities. Only two analyses resulted in significant results, possibly due to small sample sizes for most analyses. An examination of simple human presence or absence on adults and chicks on Sanibel Island (N = 448), resulted in a statistically significant effect using the Wilks' Lambda test, at the 95% confidence level (p value = 0.0419, F statistic = 2.76, d.f. = 3) (Figure 4). Specifically, there was a significant difference in PC3 (univariate p= 0.0072). The mean value for PC3 decreased from 5.5574 (N = 36, standard deviation = 12.9264) in the absence of people to -0.4856 (N = 412, standard deviation = 12.8803) in the presence of people. For chicks on Sanibel (N = 245), the presence of a vehicle also resulted in a statistically significant effect using the Wilks' Lambda test at the 99% confidence level (p value = 0.0028, F statistic = 4.82, d.f. = 3) (Figure 5). Beach-driving vehicles resulted in a significant effect in PC1 (univariate p= 0.0007); the mean value of PC1 without vehicles was -0.7708 (N = 239, standard deviation = 21.3957), whereas with vehicles it increased to 30.7054 (N = 6, standard deviation = 48.8689). Although not statistically significant (univariate p= 0.1124), for descriptive purposes it is interesting to note that PC2 decreased in this analysis from a mean 0.2569647 (N = 239, standard deviation = 15.7499820) in the absence of vehicles to -10.2357616 (N = 6, standard deviation = 23.0711386) in the presence of vehicles.

Discussion

Snowy Plover broods on Sanibel and La Costa islands showed neither increasing nor decreasing first reaction distance to humans over the thirty day period from hatch to fledge. There was also no difference in the first reaction distance between broods on Sanibel that survived to fledge and those that did not.

There was a statistically significant difference in reaction distance between Sanibel broods and La Costa broods. Pseudo-replication makes the result inconclusive with regard to the cause of this effect, but this result is encouraging nonetheless and deserves further study. It seems a reasonable possibility that the birds on Sanibel Island show increased tolerance for human presence and activity because they are exposed to continuously high levels of human disturbance. Experimental results of Flemming et al. (1998) show reduced foraging behavior of Piping Plovers broods when disturbed by people, and this is suspected as a cause of increased chick mortality; the ability to adapt to human presence, therefore, implies potentially improved chick survival rates.

Because it was impossible to run these analyses on the activity budgets data as repeated measures analyses (because individual birds were not identified), we must draw conclusions conservatively from the results of this study. Analyses of the activity budget dataset point to some shift in behavior of Sanibel birds in the presence of humans, but attempts to distinguish between the effects of different human activities were largely

unsuccessful; human presence within twenty meters of Snowy Plovers, regardless of the type of activity, resulted in altered bird behavior. In particular, the behaviors correlated with PC3, were affected; foraging and running decreased, while walking increased.

The infrequent presence of humans on La Costa beaches, leading to extremely small sample sizes, likely caused the inability to examine any meaningful differences in behaviors in the presence and absence of humans. Sample sizes were also too small with unpooled data on Sanibel to capture any differences in behavior of adults or chicks as a result of specific human activities, with the exception of the analysis of the effect of beach-driving vehicles on Sanibel chicks. For this analysis, sitting increased with PC1, while standing decreased. Although not statistically significant, the decrease in PC2 logically is important, as it indicates a potential decrease in foraging and walking in the presence of vehicles. Given the results from this study, beach-driving vehicles are obviously disruptive to Snowy Plover brood foraging behavior. They also may pose a direct threat to chick survival because chicks may be attempting to use a predator avoidance strategy, in which they sit motionless in the sand to avoid detection, when presented with a vehicle, putting them at an increased risk of being run over and crushed.

Despite the fact that the presence of humans did result in significantly different behavior in Sanibel Snowy Plovers, these birds continue to achieve fairly high nesting success and Sanibel has been a source population in recent years (SCCF, unpublished data). Given

that Snowy Plovers can and will breed and rear broods successfully in the presence of continuous human disturbance, it becomes increasingly important to tailor management strategies towards improving nesting success on all beaches across the range, rather than focusing efforts solely on “pristine” nesting habitat. To this end, there is a need to educate the public about how to minimize harmful disturbance to nesting birds and chicks when they are encountered on recreational beaches. Education and symbolic nest staking efforts should be designed to encourage public acceptance and excitement about the birds sharing the beach, thereby increasing public support for management and conservation efforts.

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Tables and Figures

Table 2. Full Bayesian hierarchical model for change in brood reaction distance over time.

	Model	Parameters
Data level	$\log(Y_i) \sim$ Multivariate normal distribution	Mean vector μ , precision matrix Ω
Constant distance	$E(\mu_i) = \beta_0$	
Linear growth	$E(\mu_i) = \beta_0 + \beta_1 x_j$	
Quadratic growth	$E(\mu_i) = \beta_0 + \beta_1 x_j + \beta_2 x_j^2$	
	$\beta_0 \sim$ Normal distribution	Mean 0, precision 0.001
	$B_1 \sim$ Normal distribution	Mean 0, precision 0.001
	$B_2 \sim$ Normal distribution	Mean 0, precision 0.001
	$\Omega \sim$ Wishart distribution	ρ degrees freedom = 17, R scale matrix = 17 X 17

Table 3. Full Bayesian hierarchical model for brood reaction distances. Vague prior and hyperprior distributions were assigned to δ , τ , η , and ϕ .

	Model	Parameters
Data level	$\log(Y_i) \sim \text{Normal distribution}$	Mean $\mu(\text{group } i, \text{ nest } j)$, precision τ
	$\tau \sim \text{Gamma distribution}$	Mean 0.001, precision 0.001
	$\mu_i \sim \text{Normal distribution}$	Mean θ , precision η
	$\eta \sim 1/\sigma^2, \sigma^2 \sim \text{Uniform distribution}$	Mean 0, precision 200
	$\theta_i \sim \text{Normal distribution}$	Mean δ , precision ϕ
	$\phi \sim 1/\sigma^2, \sigma^2 \sim \text{Uniform distribution}$	Mean 0, precision 200
	$\delta \sim \text{Normal distribution}$	Mean 0, precision 1

Table 4. Brood reaction distance change through time β values.

Node	Mean	2.50% Credible Interval	Median	97.50% Credible Interval
β_0	2.00	1.88	2.00	2.12
β_1	-0.01	-0.02	-0.01	0.00

Table 5. Brood reaction distances for fledged broods and broods that failed to fledge on Sanibel Island in meters.

Group	Mean	2.50% Credible Interval	Median	97.50% Credible Interval
Fledged Broods	6.7	6.1	6.7	7.4
Failed Broods	6.9	5.5	6.8	8.4

Figure 3. Behavioral correlates to principal components 1, 2, and 3.

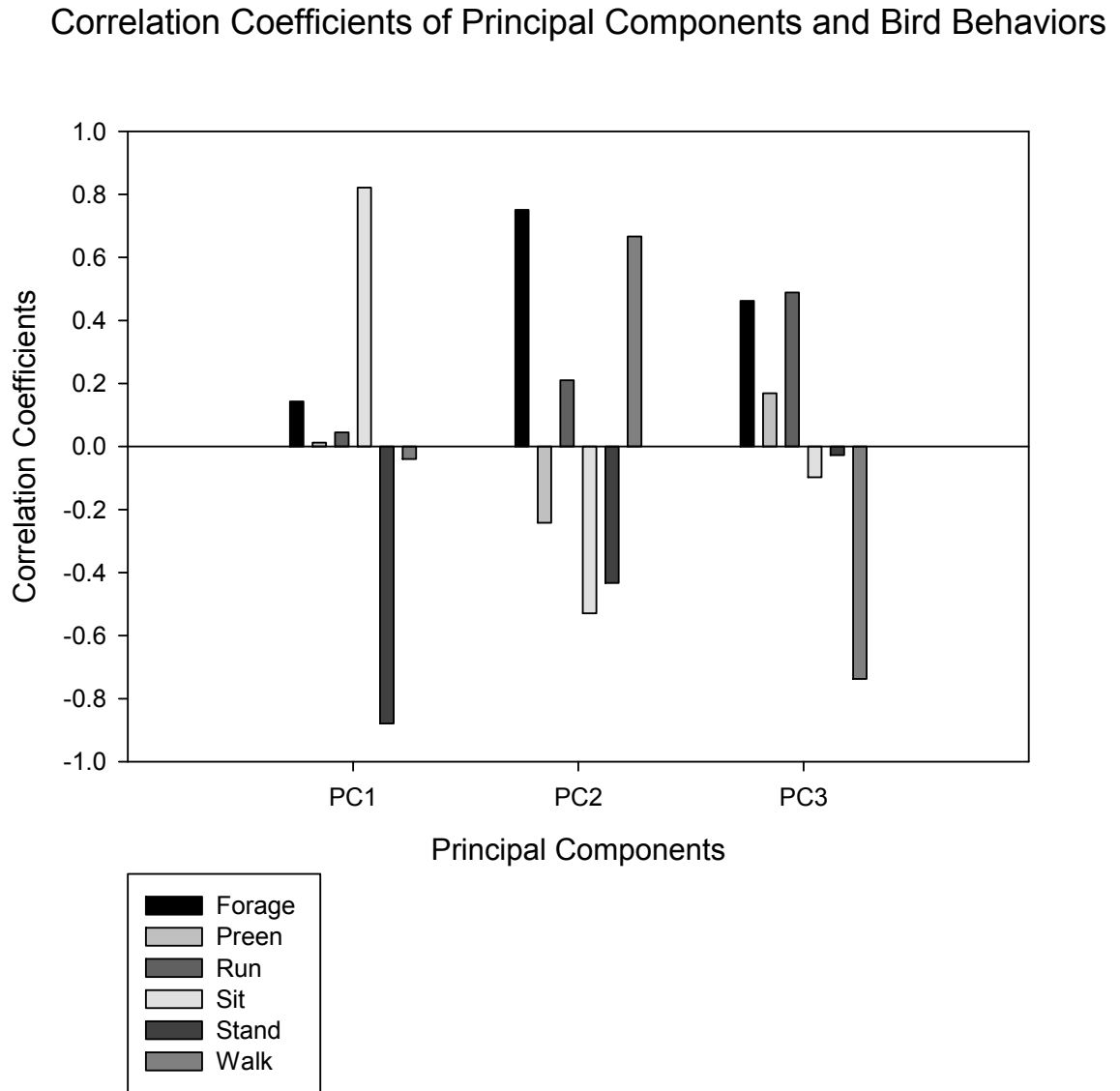


Figure 4. Principal components 1 and 3 for all Sanibel Island Snowy Plovers in the presence and absence of people.

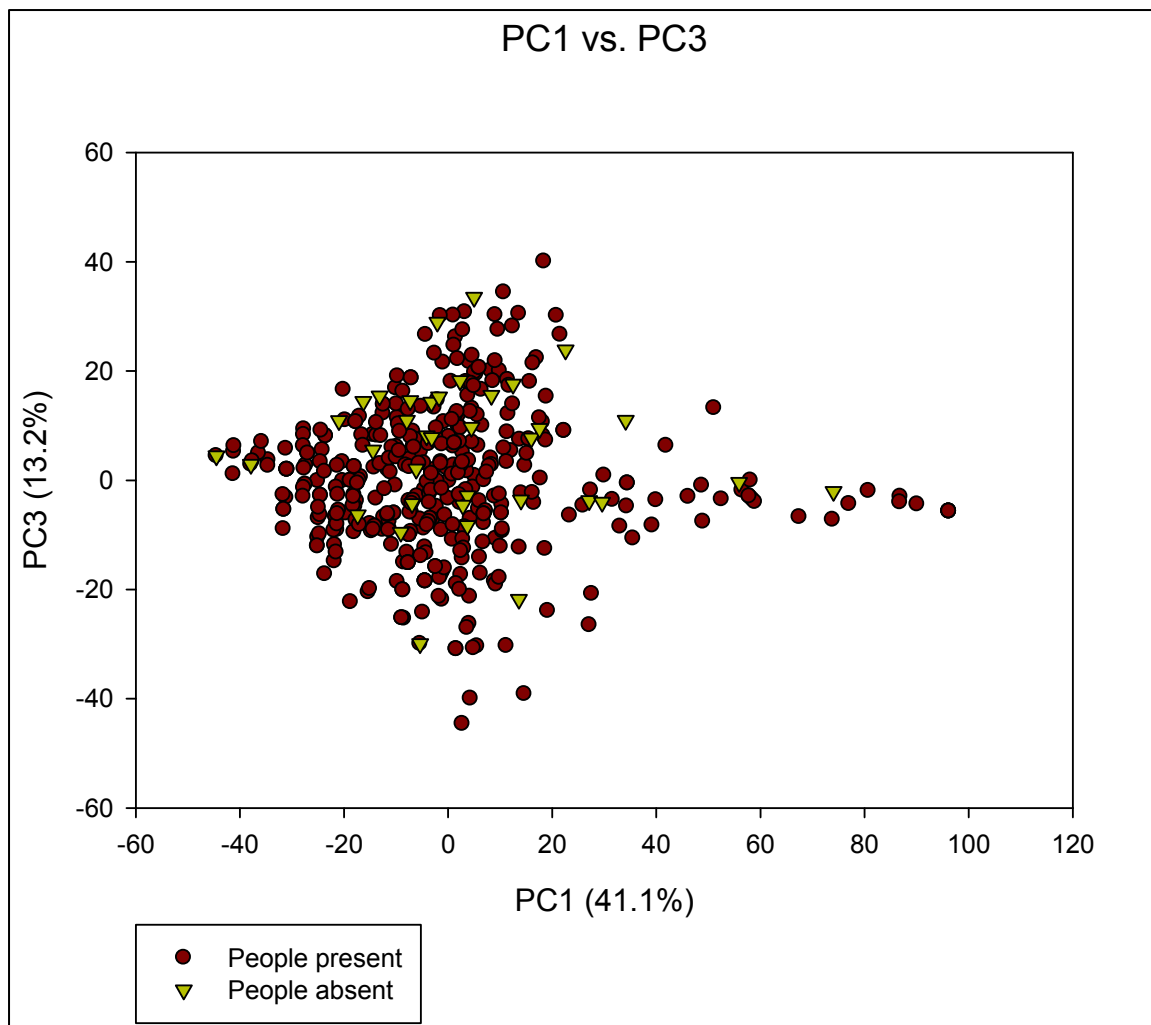


Figure 5. Principal components 1 and 2 for Sanibel Island Snowy Plover chicks in the presence and absence of beach driving vehicles.

