NOCTURNAL BEHAVIOR REDUCES PREDATION PRESSURE ON BLACK-VENTED SHEARWATERS *PUFFINUS OPISTHOMELAS*

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SUMMARY

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Many seabirds are nocturnal at their colonies, and it has been suggested that this behavior avoids diurnal predators. We examined nocturnal behavior in the Black-vented Shearwater *Puffinus opisthomelas* on Natividad Island, Mexico, to test the hypothesis that the current function of nocturnal attendance patterns is avoidance of predation by diurnal avian predators, primarily the Western Gull *Larus occidentalis.* We examined shearwater attendance and activity patterns throughout the breeding season, including activity on the colony surface, vocalizations of shearwaters and gulls, and proportion of shearwater burrows entered per night in relation to moon phase. We used direct observations and radio telemetry to examine the behavior patterns of shearwaters in flocks formed near shore at dusk. We found that shearwater activity was restricted mostly to moonless nights when light levels were below –2.2 $\log_{10}$lux($\log_{10}L$). Fewer burrows were entered on nights with a full moon, when light levels were approximately –1.0 $\log_{10}L$, than on other nights. Predation rate by Western Gulls on shearwater models was highest during daytime (>0.0 $\log_{10}L$), intermediate during moonlight (–1.0 to –1.8 $\log_{10}L$), and lowest at complete dark (<–2.2 $\log_{10}L$). Our results support the hypothesis that a current function of nocturnal activity in the Black-vented Shearwater is avoidance of predation and indicate that an indirect effect of the behavior is reduced access to the colony.

Keywords: Shearwater, nocturnal behavior, predation, colony attendance

INTRODUCTION

It has been suggested that predation is responsible for the nocturnal colony attendance patterns that are widespread in small seabirds in the families Procellaridae and Alcidae (Warham 1990, Brooke & Prince 1991, Gaston & Jones 1998). Approximately 90% of the species in the family Procellaridae and 30% of the species in the Alcidae nest in burrows or crevices, enter and exit those burrows or crevices only at night, and are not normally on the colony surface during daylight (Lack 1968, Brooke 1990, Brooke & Prince 1991, Gaston & Jones 1998). Furthermore, a majority of these species also stop or reduce activity at the colony when the moon is visible (Mougeot & Bretagnolle 2000). Hypotheses to explain this behavior include foraging patterns (Imber 1975) and, most often, predation avoidance (Watanuki 1986, Mougeot & Bretagnolle 2000).

In the present study, we used observational and manipulative experiments to test the hypothesis that nocturnal colony attendance in the Black-vented Shearwater *Puffinus opisthomelas,* a small shearwater endemic to the Pacific Coast of North America, reduces predation by diurnal avian predators, primarily the sympatric Western Gull *Larus occidentalis.* We present data showing that an indirect cost of predation pressure by Western Gulls is the constraints that nocturnal attendance patterns impose on the shearwater. Finally, we discuss the conservation and management implications of our results.

METHODS

Study area and species

Natividad Island (27.5°N, 115.25°W), located about 5 km offshore Baja California, Mexico, supports 75,000 breeding pairs of Black-vented Shearwaters—more than 95% of the world's population (Keitt *et al.* 2003). The island is arid, with little vegetation. The shearwaters breed in a dense colony in stabilized sand dune habitat (Keitt 1998). The birds are nocturnal and nest in burrows. In normal years, egg laying begins in mid March, hatching begins in May and chicks fledge by late July. Both adults participate in the incubation and chick-rearing stages, and approximately one week after hatching the chick is left alone in the burrow while the adults forage at sea (Keitt *et al.* 2000b). The most abundant avian predator on the island is the Western Gull, with a population of approximately 2000–3000 pairs (Keitt 1998). Common Ravens *Corvus corax* (10–30 birds, depending on the season) and Peregrine Falcons *Falco peregrinus* (2–4 birds) also depredate Black-vented Shearwaters.

Shearwater and gull activity in relation to light level

Attendance and vocalizations

At three adjacent locations, we measured light level, Black-vented Shearwater activity and Western Gull activity at the colony in all moon phases from 25 April to 19 July 1997. We recorded birds spending time on the colony surface, birds in flight over the colony, and birds vocalizing at the colony.

Each observation site consisted of a partial circle with a 40 m radius. Sites were monitored twice weekly at 20-minute intervals from approximately 30 minutes after sunset until 30 minutes before sunrise. Every 20 minutes, we quickly scanned the sites once using a 500,000-candle spotlight with a 30-degree beam, counting the number of shearwaters and Western Gulls visible on the ground. This technique mimicked the effect of the lighthouse on the island, which has been illuminating parts of the island every 30 seconds for the past 40 years. Observations with an infrared scope indicated that bird behavior did not change when the spotlight passed over a bird. To quantify vocalization rate, we counted the number of shearwater and gull calls for a two-minute period once every 20 minutes. To quantify flight activity, we counted all shearwaters and gulls that flew through a vertical plane extending 40 m in front of the observer for a two-minute period once every 20 minutes. Ambient light level was measured at least every 60 seconds as log lumens per square metre ($\log_{10}L$) using an Onset StowAway L1 light intensity meter (Onset Computer, Bourne, MA, USA). This meter is accurate to 0.01 $\log_{10}L$ and has a minimum reading of –2.56 $\log_{10}L$.

Predation

To test the relationship between predation intensity in the colony and light level, we conducted predation trials with mounted Black-vented Shearwater skins positioned to mimic live birds resting on the ground (live-mounts). We conducted 76 predation trials on Natividad Island from 28 May to 18 July 1997. Black-vented Shearwater live-mounts were placed in randomly selected sites in the colony and left under a cardboard box for 30 minutes before being uncovered by pulling a string attached to the box. The box was used to minimize any effects of human presence near the live-mounts at the beginning of the trial. Live-mounts were left out for 2.5 hours or until they were attacked by a Western Gull. Live-mounts were monitored from a distance of more than 50 m for the duration of the trial, except during complete darkness when the live-mounts were not visible. For those trials, live-mounts found displaced at the end of the 2.5 h trial were considered depredated. That assumption was reasonable because, during the other trials, the live-mounts were attacked vigorously and clearly displaced by Western Gulls.

Indirect costs of nocturnality

We used toothpicks placed in the entrances of shearwater burrows to test the relationship between shearwater nest attendance and moon phase. Shearwaters knock upright toothpicks down as they enter or exit the burrow, giving a measure of the percentage of burrows entered per night. Burrows with undisturbed toothpicks and those with undetermined status were counted as not entered. Fifty burrows with breeding birds were followed from 10 April to 21 July 1997. For regression analysis we assigned each day of the lunar cycle a number from 1 through 14, following Mougeot and Bretagnolle (2000). Thus, 1 represents a full moon; 7, a quarter moon, waxing or waning; and 14, a new moon.

Nearshore flocks

Black-vented Shearwaters form dense flocks sitting on the water between 100 m and 4000 m from the island (Keitt *et al.* 2000b). To determine the arrival pattern of flocking shearwaters, we surveyed the flocks from shore using a 20× Nikon spotting scope. We scanned the horizon every 20 min, beginning three hours before sunset until it became too dark to see the flocks. We counted the number of flocks and estimated the number of birds in each flock. In 1997, 15 surveys were conducted from 21 April to 14 July and in 1998, eight surveys were conducted from 27 May to 11 June.

Individual behavior in nearshore flocks

Because we could not observe flocks after sunset, we attached radio transmitters to a sample of 12 birds to determine how long birds remained in flocks before returning to the colony. We used five-minute epoxy to attach the transmitters to the area between the scapulars. Transmitters weighed approximately 15 g, less than 5% of adult body weight. One adult each from 12 breeding pairs was tagged in mid May 1998, concurrent with the late incubation period. Only three birds provided useful data on behavior.

We scanned for transmitter signals from the highest point in the colony, approximately 150 m above sea level. Scans of all transmitter frequencies were conducted every 30 minutes. If a signal was heard from a bird near shore, we listened continuously to determine an accurate arrival time at the colony. Because the transmitter signal stops when a bird is submerged, we were able to determine from the signal pattern whether a bird was loafing (constant signal) or diving/foraging (broken signal). We assumed that a constant signal indicated a non-foraging bird because Black-vented Shearwaters are accomplished divers (Keitt *et al.* 2000a), and even in surface-feeding events, we assumed that the shearwaters would partially submerge and disrupt the signal. We distinguished between birds on the water and birds on the colony by signal strength and direction.

Statistical analyses

Statistical analyses were run using Systat 7.0 (SPSS, Chicago, IL, USA). Results are reported as mean ± standard deviation and considered significant at $P < 0.05$.

RESULTS

Shearwater and gull activity in relation to light level

Attendance and vocalizations

All three measures of activity (numbers of birds on the colony surface, birds flying, and vocalizations) indicate that shearwaters were almost exclusively active at the colony during periods of complete darkness (<–2.2 $\log_{10}L$; Fig. 1). Shearwaters were first seen on the colony shortly after measured light level dropped below –2.2 $\log_{10}L$, and activity continued unabated until shortly before the light level rose above that threshold. The probability of encountering each of the observed behaviors increased dramatically as light levels fell and approached the threshold of –2.2 $\log_{10}L$ (Fig. 1). In contrast, Western Gulls were more active when light levels were >–2.2 $\log_{10}L$, and their activity was greatest when the shearwaters were least active (Fig. 2).

Predation

Attacks on Black-vented Shearwater live-mounts were highest during daylight, intermediate during moonlight, and lowest on dark nights (2×3 contingency table, $P < 0.001$; Fig. 3).

Indirect costs of nocturnality

The percentage of burrows entered per night was lower on or near the full moon. Moon phase was responsible for 96% of the variation in the proportion of burrows entered ($F_{12,1} = 318.2$, $R^2 = 0.96$, $P < 0.001$; Fig. 4). Only 40%–60% of burrows were entered on the full moon and the two nights on either side of the full moon. More than 80% of burrows were entered on most other nights.

Nearshore flocks

We observed flocks on 74% of the surveys. We frequently saw several groups of 1000–2000 birds, with a maximum number of about 5000 rafting birds. Flocks began arriving on the water near the colony between 10 minutes and 140 minutes before sunset, with the average time of arrival being 89 minutes before sunset (± 35 minutes, n = 15 flocks).

Individual behavior in nearshore flocks

We were able to track three radio-tagged birds during their arrival at the colony. Those birds arrived in the waters near the island by 17h00, 18h30, and 21h00 and flew to the island at 20h45, 20h55, and 02h30 respectively. The first two arrivals occurred on nights without moonlight. On those nights, the birds arrived in the nearshore waters before sunset and loafed on the water without feeding for 215 minutes and 145 minutes respectively, entering the colony less than 30 minutes after the light level dropped below –2.2 $\log_{10}L$. The third bird arrived on a waxing 2/3 moon, which set at 02h10. That bird spent approximately 5.5 hours near shore, entering the colony shortly after moonset, within 30 minutes of the light level falling below –2.2 $\log_{10}L$. Transmitter signal patterns indicated that this bird was not foraging while waiting on the water. We did not collect any details on the timing of birds departing the colony.

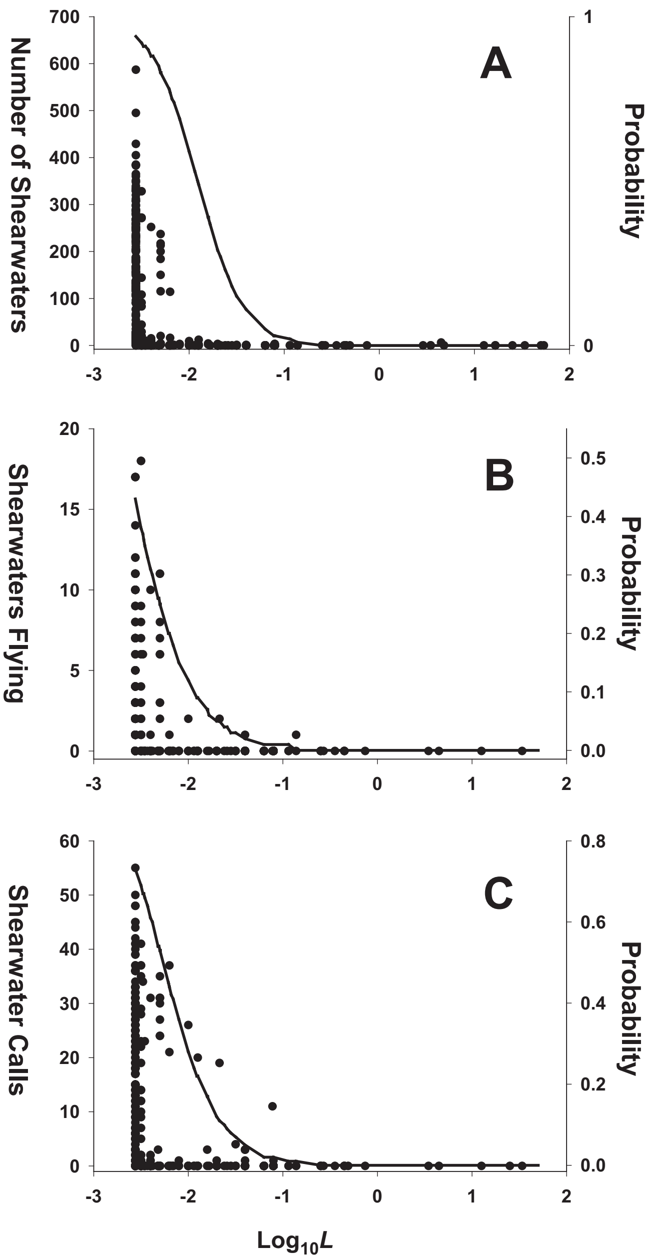

Fig. 1. Activity of Black-vented Shearwaters in relation to light level. Logistic regressions represent the probability of encountering at least one shearwater (A) on the surface of the colony, (B) flying, (C) vocalizing at the corresponding light level.

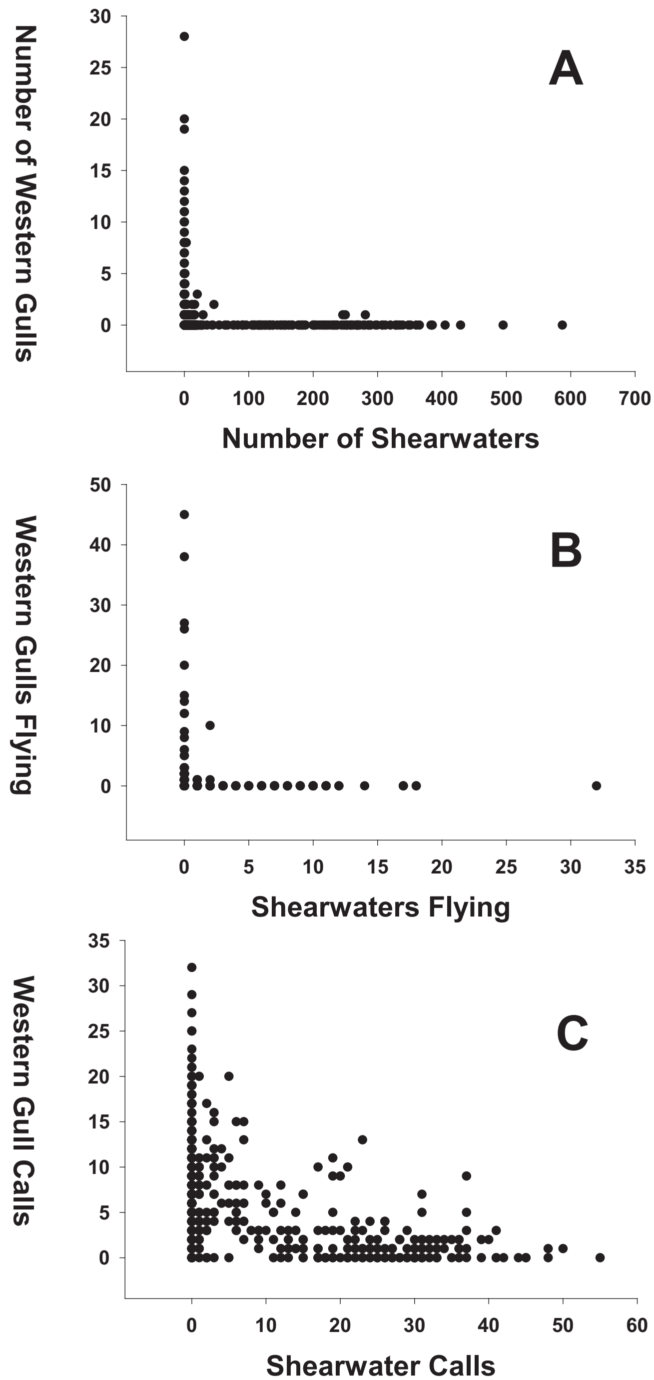

Fig. 2. Activity of Black-vented Shearwaters in relation to Western Gulls for (A) number of birds on the surface of the colony, (B) flying, (C) vocalizing.

DISCUSSION

Our data support the hypothesis that a current function of nocturnal activity patterns in the Black-vented Shearwater is reduction in the likelihood of predation by Western Gulls because

- Black-vented Shearwater activity was limited almost exclusively to periods of complete darkness.
- Black-vented Shearwaters were most active when the most abundant predator at the colony, Western Gulls, were least active.
- predation risk was highest when the shearwaters were least active.

We used shearwater live-mounts as a proxy for measuring actual predation by gulls on Black-vented Shearwaters. We observed Western Gulls attacking a live shearwater on only one occasion. On two other occasions, we observed shearwaters on the colony during daylight and both were being attacked by Common Ravens. We observed gulls eating freshly killed shearwaters almost daily, but it was impossible to determine whether the shearwaters were actually killed by the gulls or if they were being scavenged after being killed by other predators such as feral cats (*Felis catus*) or Peregrine Falcons. Peregrine Falcons are diurnal predators and have the capacity to catch shearwaters at sea and to return to the colony.

Gulls are regular predators of *Puffinus* shearwaters on their colonies (Warham 1990). Manx Shearwaters *Puffinus puffinus* (450–500 g) are depredated by Greater Black-backed Gulls *L. marinus* (1000–1200 g), Herring Gulls *L. argentatus* (1000–1200 g) and Lesser Black-backed Gulls *L. fuscus* (830 g) (Corkhill 1973, Brooke 1990). Western Gulls (800–1100 g) should therefore be fully capable of depredating Black-vented Shearwaters (410 g).

Activity of Black-vented Shearwaters—measured as number of birds on the colony, number of birds in flight, and vocalization frequency—was virtually zero in all light conditions >–2.2 $\log_{10}L$. Western Gulls, in contrast, were most active when light conditions were >–2.2 $\log_{10}L$. The threshold light level of –2.2 $\log_{10}L$ was constant throughout the three-month study in 1997 and 1998. These results agree with the findings of Watanuki (1986) for Leach's Storm-Petrels *Oceanodroma leucorhoa* and Mougeot & Bretagnolle (2000) for Blue Petrels *Halobaena caerulea* and Thin-billed Prions *Pachyptila belcheri.*

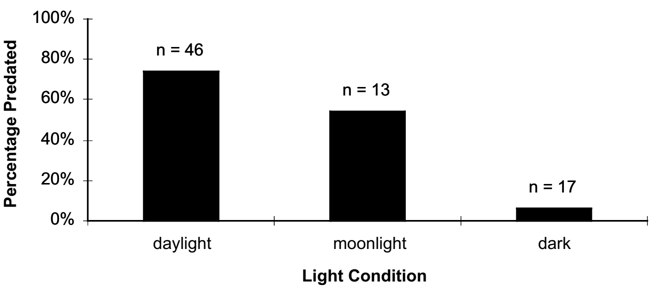

Fig. 3. Percent of shearwater live-mounts attacked by Western Gulls during daylight (>0.0 $\log_{10}L$), moonlight (–1.0 to –1.8 $\log_{10}L$), and night (<–2.2 $\log_{10}L$). All treatments differed significantly (2xxby3 contingency table, $P < 0.001$).

Predation risk for shearwater live-mounts was significantly higher at light levels above the threshold of –2.2 $\log_{10}L$. Despite the increased risk, some Black-vented Shearwaters still attended the colony when light levels were above that threshold, based on our data for burrow attendance and observations. However, those birds appeared to minimize predation by engaging in low-risk behaviors. For example, the birds were quiet, they quickly entered their burrows after landing on the colony, and they tended to loaf only in the entrance of a burrow (BSK pers. obs.). Manx Shearwaters that attended their colony during moonlight also appeared to minimize predation risk by engaging in inconspicuous behaviors (Storey & Grimmer 1986). In addition, on nights with a full moon, when the light level never fell below the threshold, we observed Black-vented Shearwaters on the colony only at the darkest time of night: either 45 minutes after sunset and before the moon had risen far above the horizon, or 45 minutes before sunrise and after the moon had reached the horizon.

Indirect effects of predation pressure

Lima (1998) reviewed the non-lethal effects of predation risk and concluded that predators may limit their prey's access to food, leading to reduced body condition. Our study demonstrates an additional effect of predation: reduced access to breeding sites and potential limitation on the chick's access to food. Threat of Western Gull predation indirectly affects Black-vented Shearwaters in three ways:

- When the moon is full, safe access to the burrow for incubation shift exchanges or chick-feeding events is reduced.
- On nights when the moon is present, the number of hours of safe access to the burrow is reduced.
- The amount of time spent in offshore rafts is increased, which presumably is more costly than coming directly to the burrow to feed and rest.

So instead of leading to reduced feeding opportunities (as in Lima 1998), predation pressure in this case possibly causes reduced access to the burrows. The result could be increased energy expenditure by birds waiting offshore to enter the colony, fewer

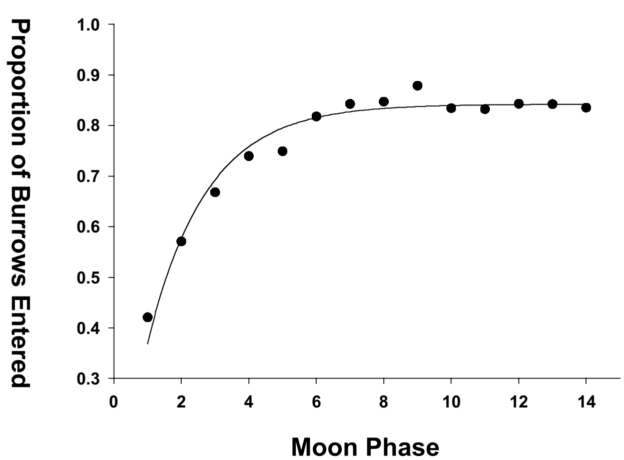

Fig. 4. Proportion of burrows entered in relation to moon phase for early incubation through late chick-rearing in 1997 (100 nights). Moon phase is separated into 14 categories, each representing one day between a new and a full moon. 1 = full moon; 7 = quarter moon waxing or waning; 14 = new moon ($F_{12,1} = 318.2$; $R^2 = 0.96$, $P < 0.001$).

chick-feeding opportunities, and increased difficulty of scheduling incubation shift exchanges. However, it is interesting that access to burrows is reduced only on about three nights per moon cycle (full moon and the day before and after; Fig. 3), and even on those nights, 40%–60% of burrows are entered. So, although the timing of access is definitely limited, predation threat does not appear to greatly reduce the number of nights on which shearwaters can enter their burrows.

The formation of rafts in the nearshore waters of colony islands at dusk is common in many shearwater species (Warham 1990). Black-vented Shearwaters frequently formed rafts in the nearshore waters of Natividad Island. Our radio telemetry data were limited, but they provided important information on the behavior of individuals within the flocks. It is likely that the birds are coming from distant foraging grounds and hence are unable to precisely time their return to the colony. Those arriving early must therefore wait until it is safe to land. Our data show that flocks formed an average of 89 minutes before sunset and that birds arrived at the colony about 30 minutes after sunset, yielding an average period of rafting of about 120 minutes. On nights with a waxing moon, that period of waiting to come ashore apparently can be greatly increased: we observed one bird waiting for 5.5 hours.

Warham (1990) reported that most procellarids in nearshore rafts do not feed unless schooling fish are present. Our radio telemetry data indicated that these birds were not actively feeding while waiting in the nearshore waters. We did observe some feeding by Black-vented Shearwaters in the nearshore waters of the colony, but such feeding was rare and tended to occur late in the breeding season (BSK pers. obs.).

Predation pressure is not the only possible explanation for the prevalence of nocturnal behavior in seabirds. Even in the absence of predators, some seabirds maintain nocturnal behavior (e.g. Wedge-tailed Shearwater *P. pacificus* and Bonin Petrel *Pterodroma hypoleucus* in the gull-free Hawaiian Islands). However, those species are generally less strict about their nocturnal behavior than the Black-vented Shearwater: i.e. they are not lunar phobic, and they enter the colony at dusk (BSK pers. obs.). Furthermore, there is even intraspecific variation in nocturnal and lunar-phobic behavior. For example, the Cory's Shearwater *Calonectris diomedea* is nocturnal at most of its colonies (Klomp & Furness 1992), yet diurnal on at least one colony (Hamer & Read 1987). The Wedge-tailed Shearwater also displays nocturnal activity at some colonies and diurnal activity at others (Whittow 1997). This variation among populations suggests that nocturnal behavior is a plastic trait and that some factor—predation or other—is necessary to maintain the behavior.

Our data are not compatible with the foraging hypothesis as an explanation of nocturnal behavior in Black-vented Shearwaters. Briefly, the foraging hypothesis outlined by Imber (1975) suggests that colony attendance patterns of seabirds are regulated by food availability at sea. Our predation avoidance conclusion is most strongly supported by the radio telemetry data that showed birds waiting, without feeding, in the nearshore waters until light levels fell below the established "safe" threshold.

Other studies have provided evidence to support the foraging hypothesis as an explanation for nocturnal colony attendance. For example, Klomp and Furness (1992) found that more Cory's Shearwater chicks (*c.* 80%) were fed before midnight on dark nights than on full-moon nights (*c.* 15%) and that the mass of food deliveries to chicks was greater on dark nights than on full-moon nights. Those authors concluded that forage availability was reduced during moonlit nights. However, such observations are not necessarily incompatible with the predation hypothesis. For example, our radio telemetry data showed that, on moonlit nights, Black-vented Shearwaters loafed in the nearshore waters for much of the night and arrived at the colony to feed their chick only after it was "safe" to do so. Furthermore, the reduced chick meal size found by Klomp and Furness could be explained in this case by the increased digestion and processing of the meal during the time the birds were rafting in nearshore waters.

CONCLUSIONS

Our data indicate that nocturnality in Black-vented Shearwaters reduces their susceptibility to Western Gull predation. Furthermore, the threat of predation appeared to reduce the period of safe access to the colony to nighttime when the moon was absent. Shearwaters that did attend the colony on moonlit nights did so during the darkest period of the night and demonstrated behaviors that apparently reduce predation risk.

Management implications

The negative effects of anthropogenic light on nocturnal birds are well established. However, researchers have focused almost exclusively on the mortality associated with light attraction (e.g., Reed *et al.* 1985). To our knowledge no one has addressed the potential for anthropogenic light to increase predation pressure and limit access to the colony. If Black-vented Shearwaters avoid attending the colony because of threat of Western Gull predation when the light level is above $-2.2 \log_{10}L$, then other small nocturnal seabirds breeding sympatrically with Western Gulls should also avoid the colony when the light level is above that threshold. Consequently, anthropogenic light sources that illuminate a colony above $-2.2 \log_{10}L$ could affect seabirds in two ways:

- Increased predation
- Decreased access to the colony, and thus decreased foraging efficiency and ability to feed chicks

Increased predation on adults is particularly problematic because the life-history characteristics typical of petrels and many alcids (low adult mortality and low reproductive rate) mean that even small increases in adult mortality can lead to negative population growth (Russell 1999).

Commercial squid fishing vessels use extremely bright lights to attract squid to the surface. Other commercial fishing vessels often use bright lights to illuminate the work deck. On moonless nights both types of vessel can raise light levels on island seabird colonies above $-2.2 \log_{10}L$ (Keitt unpubl. data). When anchored offshore, small squid fishing boats can increase light levels on a colony to above $-2.2 \log_{10}L$ from up to 800 m away. Larger squid fishing vessels may have a much greater sphere of influence.

Research on the response of gulls and nocturnal seabirds to increased anthropogenic light levels is needed to properly regulate such light sources near colonies of seabirds. In particular, it is critical to know if birds return to the colony on moonless nights even in the presence of anthropogenic light $>-2.2 \log_{10}L$, and if gull predation is greater under this artificial light.

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Black-vented Shearwater on the colony. photo: Brad Keitt

The town on Natividad Island, Mexico: the shearwater colony occupies a 2.5 km squared area extending behind the town. photo: Brad Keitt