NOCTURNAL COPULATION IN GLAUCOUS-WINGED GULLS LARUS GLAUCESCENS

FLOYD E. HAYES1* & JAMES L. HAYWARD2

1Department of Biology, Pacific Union College, Angwin, California 94508, USA 2Department of Biology, Andrews University, 4280 Administration Drive, Berrien Springs, Michigan 49104-0410, USA

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ABSTRACT


Gulls (Laridae) are primarily diurnal, although many species forage opportunistically at night, and several species copulate at night. We used trail cameras to study time-of-day variation in the rate of copulation by Glaucous-winged Gulls Larus glaucescens in a breeding colony (1500+ pairs) at Protection Island, Washington, USA, from 31 May to 07 June 2018. Copulations (n = 353) occurred at a significantly higher rate during the day (0.82/camera-h) than at night (0.51/camera-h), with 76.3 % of copulations during the day and 23.7 % at night (daylight comprised 66.1 % and darkness comprised 33.9 % of the study period). The copulation rate peaked shortly before and after dawn, with a second peak before sunset. Copulation rate was lowest during the middle of the day and middle of the night. Glaucous-winged Gulls sleep intermittently during both day and night and have sufficient energy to sustain sporadic copulations during the night, which appears to be a normal part of their reproductive behavior. The most likely advantage of this pattern is an increased opportunity for fertilization with a mate.

Key words: behavior, cathemeral, Laridae, life history, mating, nocturnality, reproduction

INTRODUCTION

Because the study of bird behavior at night requires specialized optical equipment and is logistically challenging (Allison & DeStafano 2006), most studies of birds occur during daylight. A full understanding of avian behavior and ecology, however, requires the study of nocturnal activity. Many species of birds considered to be diurnal occasionally exhibit nocturnal activities such as vocalizing, foraging, and migrating (Martin 1990, McNeil et al. 1992, 1993; Newton 2008, La 2011). Some waterbirds that are primarily diurnal are known to extend reproductive activities such as courtship and copulation into the night. These include several species of grebes (Podicipedidae; McAllister 1958, Hayes et al. 2018), gulls (Laridae; Howell et al. 1974, Fetterolf 1979, McNeil et al. 1993, Hébert & McNeil 1999), and shorebirds (Charadriidae; Johnson et al. 2002, 2003).

Gulls appear to be primarily diurnal, but many species forage opportunistically at night, especially on moonlit nights and under artificial lights (Nelson 1989, Burger & Staine 1993, McNeil et al. 1993, Garthe & Höppop 1996, Nocera & Kress 1996, Oro et al. 1997, Yorio et al. 2005, Leopold et al. 2010, Martin & Raim 2014, Pugh & Pawson 2016), and one species forages exclusively at night (Hailman 1964). At least six gull species are reported to copulate at night (McNeil et al. 1993), but details have been published only for the Ring-billed Gull Larus delawarensis (Fetterolf 1979, Hébert & McNeil 1999). Additional research may reveal that nocturnality in the foraging and reproductive behavior of gulls is more widespread than currently recognized.

Glaucous-winged Gulls Larus glaucescens are the most abundant larids residing along the Pacific Northwest coast of North America (Hayward & Verbeek 2008). Courtship and copulation in this species have been described and closely resemble what has been described for other gulls (Sandler 2013, McWilliams et al. 2018), including precopulatory head tossing, courtship feeding, and mew, choke, and long calls (James-Veitch & Booth 1954, Moyrihan 1955, 1962; Timbergen 1959, 1960; Vermeer 1963, Hayward & Verbeek 2008). Just before mounting, the male begins to utter a high amplitude, rhythmic copulation call, which may last for most of the interaction (McWilliams et al. 2018). This call socially facilitates reproductive behavior among other members of the breeding colony (Atkins et al. 2017). Copulation frequency increases gradually during the mating season, followed by a more rapid decline once egg-laying is complete (McWilliams et al. 2018).

In this paper, we document time-of-day variation in the rate of copulation by Glaucous-winged Gulls, which had previously been reported to copulate at night but without details (McNeil et al. 1993). We also evaluate eight hypotheses for why individuals may potentially benefit from nocturnal copulation instead of simply sleeping throughout the night (Hayes et al. 2018): (1) to exploit elevated light levels; (2) to avoid daylight disturbance; (3) to avoid diurnal predation; (4) to avoid high temperatures on hot days; (5) to avoid sexual interference; (6) to engage in extrapair copulations; (7) to exploit abandoned nests; and (8) to increase opportunities for fertilization with a mate.

METHODS

Study area

Data were collected from 31 May to 07 June 2018 at a Glaucous-winged Gull colony on Violet Point, Protection Island National Wildlife Refuge (48°07′40″N, 122°55′03″W), Jefferson County, Washington, USA. Protection Island is 1.5 km² in area and is centrally located in the Salish Sea near the east end of the Strait of Juan de Fuca. Only two humans permanently reside on the island.
Gulls nest among herbaceous plants and driftwood. During this study, the colony contained more than 1500 breeding pairs (Henson et al. 2019). Gulls typically arrive on the colony in February and remain through late September (Hayward et al. 2017). Copulation is frequent from mid-May to late June (McWilliams et al. 2018); egg-laying begins in late May and continues through late June (Vermeer 1963, Hayward & Verbeek 2008).

The Protection Island colony occurs within a Glaucous-winged Gull × Western Gull *L. occidentalis* hybrid zone (Bell 1996). A few Western Gulls reside on the island, but most of the residents are hybrids. Because most of the hybrids exhibit more phenotypic features of the Glaucous-winged Gull than the Western Gull (Bell 1996, Moncrieff et al. 2013, Megna et al. 2014), the hybrids are referred to here as Glaucous-winged Gulls.

No artificial lights illuminate Protection Island, and the colony is located 3.5 km from human sources of artificial light on the mainland.

**Sampling methods**

We deployed three trail cameras (Bushnell Trophy Cam Bone Collector RTAP Night Vision and Bushnell Trophy Cam HD Aggressor No Glow; Bushnell Corporation, Overland, Kansas, USA) along the southern edge of the Violet Point gull colony, where dense nesting occurs among driftwood above the south beach. Each camera was attached to driftwood with duct tape and pointed toward a different section of the colony so that the fields of view, which included dozens of courting gulls, did not overlap. Cameras were programmed to take photos at regular intervals of 1 min (one camera) or 5 min (two cameras; the different intervals resulted from an error in setting the cameras). The total number of photos obtained per h (84) by all three cameras remained constant, for a cumulative total of 13 776 photos for the 8-d study period.

We subsequently evaluated each photo to identify copulation events, broadly defined as one individual mounting another individual (Barrows 2011) regardless of success. We recorded the time of day for each copulation and whether it occurred during day (sunrise to sunset) or night (sunset to sunrise), based on sunrise and sunset data at the United States Naval Observatory website (www.usno.navy.mil/USNO). To consistently compare the frequency of copulations during day and night, we reexamined each photo of diurnal copulation and removed copulation events judged to be too distant (beyond ca. 10 m) to be detected at night due to the limited distance of the cameras’ infrared flash.

We obtained data for several environmental variables that potentially influenced time-of-day variation in copulation behavior. Data on lunar illumination (percent illumination of the moon) were obtained for midnight of each night during the study period from the United States Naval Observatory website (www.usno.navy.mil/USNO). Temperature and precipitation data were obtained from weather station KWAPORT20, located 11.9 km E of Protection Island, at Port Townsend, Washington (www.wunderground.com). Based on photos from the camera taking photos at 1 min intervals, we recorded the time for each disturbance at the colony, defined as > 50 % of the gulls departing the colony within 50 m of the camera’s view.

**Statistical analysis**

A chi-square analyses ($\chi^2$ statistic; Zar 2010) was used to compare the proportions of diurnal and nocturnal copulations recorded among the three cameras to assess whether the proportion of nocturnal copulations varied in different areas of the breeding colony. A Mann-Whitney U test ($z$ statistic; Zar 2010) was used to compare the rate of copulation between day and night based on the number of copulations recorded each hour during day and night, respectively, but excluding the periods of 05h00–05h59 (when sunrise occurred) and 21h00–21h59 (when sunset occurred), for the camera in which photos were taken at 1-min intervals. The statistical tests were calculated with Statistix 10 software (Anonymous 2013).

**RESULTS**

The three cameras consistently captured photos of the colony during 164 h, from 11h00 on 31 May to 07h00 on 07 June. Evaluation of the photos revealed 425 copulations during 492 camera-h. After eliminating 72 diurnal copulations judged to be too distant to
be detected at night, our final sample size was 353 copulations. Because the proportions of diurnal and nocturnal copulations did not differ significantly among the three cameras at different sites within the colony ($\chi^2 = 2.42, df = 2, P = 0.30$), the data were pooled for further analyses.

Copulations occurred throughout each day and night (Figs. 1, 2) at a rate of 0.82/camera-h during the day and 0.51/camera-h at night. The cameras recorded 18 h of data for each of three hourly periods of the day (07h00–10h59) and 21 h of data for each of the remaining 21 hourly periods of the day. After an adjustment (by extrapolation) was made to equalize sampling effort for each hourly period, we found that 76.3 % of copulations occurred during the day, which comprised 66.1 % of the study period, and 23.7 % of copulations occurred at night, which comprised 33.9 % of the study period. The copulation rate peaked shortly before and after dawn, with a second peak before sunset. Copulation rate was lowest during the middle of the day and middle of the night (Fig. 2). Based on data from the camera in which photos were taken at 1-min intervals, the number of copulations/h was significantly greater during the day ($n = 101$) than at night ($n = 49; z = 2.66, P = 0.008$).

Temperatures during the study period ranged from 8.7–21.2 °C, with copulations occurring at all temperatures ranging from 8.7–21.2 °C. Light rainfall (11.7 mm in nearby Port Townsend) and light fog occurred intermittently during two days but did not obstruct the cameras’ views of gulls, and copulations occurred during these periods. Lunar illumination during the study period ranged from 45 %–93 %. Glaucous-winged Gulls copulated throughout the night of 06–07 June, when lunar illumination was lowest (45 %).

The cameras recorded 17 disturbance events in which > 50 % of the gulls within 50 m in front of a camera departed, with a rate of 0.04 disturbances/h during the day ($n = 4$) and 0.23 disturbances/h at night ($n = 13$). Most disturbances lasted < 1–2 min and none lasted > 3 min; assuming an average length of 2 min, disturbances occurred during 0.12 % of the day and 0.40 % of the night. However, copulations did not resume until at least 13 min after a disturbance. The causes of the disturbances were not obvious from the photos but were presumably caused by approaching predators. On eight occasions during the day, a human researcher slowly approached the camera while counting nests containing eggs, but only gulls within 5 m of the researcher moved out of the way, and gulls returned within 1–2 min. Copulations resumed as quickly as 6 min after a human departed.

**DISCUSSION**

Our data reveal that Glaucous-winged Gulls are relatively cathemeral (active both day and night) in their copulation behavior, but with a preference for crepuscular times. Nearly a quarter of copulations occurred at night, with copulation occurring at a lower rate at night than during the day. The proportion of nocturnal copulations likely varies with latitude, depending on the duration of darkness. The frequency of nocturnal copulation has been studied in only one other species of gull, the Ring-billed Gull L. delawarensis, in which copulations occurred mostly at night (79 %) in one study (Fetterolf 1979) and mostly during the day in another study (Hébert & McNeil 1999). Seven hypotheses have been proposed for why birds that are primarily diurnal potentially benefit from copulating at night (Hayes et al. 2018). We evaluate each of these hypotheses, plus an eighth hypothesis, in the discussion below.

The elevated light levels hypothesis postulates that birds extend copulation into the night during periods of elevated light levels shortly before sunrise, shortly after sunset, and on moonlit nights (Hayes et al. 2018). Although Glaucous-winged Gulls copulated when lunar illumination was lowest (45 %), it remains unknown whether copulation occurs on moonless nights. However, copulation during moonless or nearly moonless nights (0 % to 16 %) has been reported in two species of shorebirds (Johnson et al. 2002) and two species of grebes (Hayes et al. 2018).

The avoidance of daylight disturbance hypothesis proposes that birds engage in nocturnal reproductive activities because human disturbances during daylight disrupt their normal reproductive activities (Hayes et al. 2018). However, human disturbances in the Protection Island gull colony, and in grebe colonies in California, where copulation frequently occurs at night (Hayes et al. 2018), are minimal and exert a trivial effect on reducing the time engaged in diurnal reproductive activities. Gulls on the Protection Island colony commonly copulate within 10–20 m of human research activity.

The avoidance of diurnal predation hypothesis posits that birds engage in nocturnal reproductive activities to avoid diurnal predators or kleptoparasites that steal food carried by adults to their young. This appears to be case with many seabirds, especially the smaller species (Brooke & Prince 1991, McNeil et al. 1993). Bald Eagles Haliaeetus leucocephalus frequently prey on Glaucous-winged Gull chicks and adults at Protection Island (Galusha & Hayward 2002, Hayward et al. 2010), and their disturbances cause immediate bouts of preening (Henson et al. 2012) and suppress copulation (Atkins et al. 2017). However, only four diurnal disturbances, most likely caused by Bald Eagles, occurred during the study period, in contrast to 13 nocturnal disturbances. Northern River Otters Lontra canadensis are present on Protection Island and are known to prey on Glaucous-winged Gull chicks and adults elsewhere, usually at night (Hayward et al. 1975, Footit & Butler 1977, Verbeek & Morgan 1978). Therefore, it is possible that this otter species may have caused the nocturnal disturbances. Panic flights at night are a normal reaction to nocturnal predators for at least some species of gulls (Southern & Southern 1979, Southern et al. 1982), including Glaucous-winged Gulls (Hayward et al. 2010). Because more disturbances, presumably by predators, occur at night than during the day, nocturnal copulation does not appear to be a strategy to avoid diurnal predation.

The heat avoidance hypothesis proposes that birds avoid energetically demanding and heat-generating reproductive activities during hot days by postponing them until night, when temperatures are cooler (Howell et al. 1974). Gray Gulls Leucophaeus modestus court and copulate during the day along the coast of Chile. However, in nearby deserts where they nest, Gray Gulls conduct their reproductive activities at night to avoid extremely hot daytime temperatures (Howell et al. 1974). In our study, the temperature never exceeded 22 °C and copulation occurred during the warmest period of the day.

The avoidance of sexual interference hypothesis proposes that male birds copulating at night are interrupted (knocked off the female) less frequently than during the day (Fetterolf 1979). Sexual interference occurs less frequently in Ring-billed Gulls copulating at night (Fetterolf 1979, Hébert & McNeil 1999). However, sexual interference has never been reported in Glaucous-winged Gulls and was not detected during this study.
The extrapair copulations hypothesis posits that birds may seek extrapair copulations under the cover of darkness, reducing the probability of detection and retaliation by their social mates (Hayes et al. 2018). Extrapair copulation has been reported for Glaucous-winged Gulls (Salzer & Larkin 1990), but this hypothesis would be extremely difficult to evaluate without well-marked individuals that can be distinguished in low-resolution night photos.

The exploiting abandoned nests hypothesis postulates that birds may benefit by copulating or usurping or dumping eggs on recently vacated nests in which eggs disappeared or were hatched (Hayes et al. 2018). Although this appears to be a strategy used by grebes during both day and night (Hayes et al. 2018), Glaucous-winged Gulls do not copulate on nests (McWilliams et al. 2018).

There is no evidence supporting any of the above hypotheses for why nocturnal copulation may be advantageous for Glaucous-winged Gulls. The most likely advantage is an increased opportunity for fertilization with a mate, which we propose as an eighth hypothesis. Nocturnal copulation may represent a normal aspect of the reproductive behavioral repertoire of Glaucous-winged Gulls, which sleep intermittently throughout the day (Henson et al. 2007) and night (photographic evidence from this study), and apparently have sufficient energy to sustain sporadic copulations during the night.

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REFERENCES


