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NOCTURNAL COPULATION IN GLAUCOUS-WINGED GULLS *LARUS GLAUCESCENS*

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ABSTRACT

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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 & Hüppop 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, Moynihan 1955, 1962; Tinbergen 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 km^2 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 KWAPORTT20, 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 (χ^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

Fig. 1. Nocturnal copulation by a pair of Glaucous-winged Gulls at 01h21 on 02 June 2018 at Protection Island, Washington, USA.

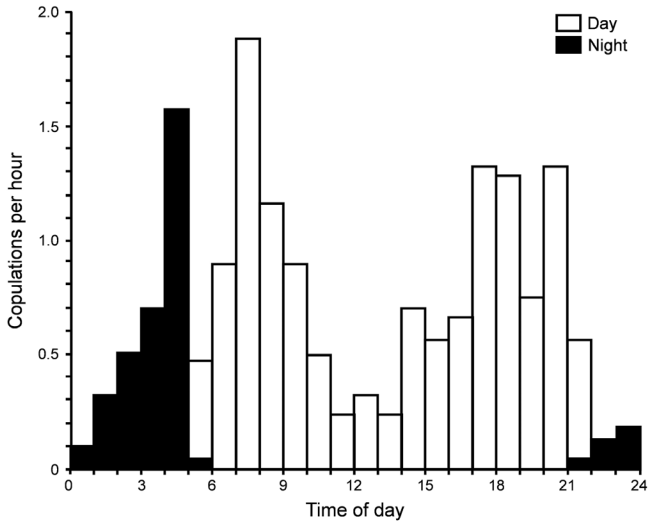

Fig. 2. Time-of-day variation in the frequency of gull copulations (*n* = 353) during 31 May to 07 June 2018 at Protection Island, Washington, USA.

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 ($X^2 = 2.42$, $df = 2$, $P = 0.30$), 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 cameras 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%–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, Foottit & 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 from 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 postulates 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 and 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

ALLISON, N.L. & DESTEFANO, S. 2006. Equipment and techniques for nocturnal wildlife studies. *Wildlife Society Bulletin* 34: 1036–1044.

ANONYMOUS. 2013. *Statistix 10 User's Manual.* Tallahassee, USA: Analytical Software.

ATKINS, G.J., REICHERT, A.A., HENSON, S.M. & HAYWARD, J.L. 2017. Copulation call coordinates timing of head-tossing and mounting behaviors in neighboring Glaucous-winged Gulls (*Larus glaucescens*). *Wilson Journal of Ornithology* 129: 560–567.

BARROWS, E.M. 2011. *Animal Behavior Desk Reference: A Dictionary of Animal Behavior, Ecology, and Evolution*. Boca Raton, USA: CRC Press.

BELL, D.A. 1996. Genetic differentiation, geographic variation and hybridization in gulls of the *Larus glaucescens-occidentalis* complex. *The Condor* 98: 527–546.

BROOKE, M.D.L. & PRINCE, P.A. 1991. Nocturnality in seabirds. *Proceedings of the International Ornithological Congress* 20: 1113–1121.

BURGER, J. & STAINE, K.J. 1993. Nocturnal behavior of gulls in coastal New Jersey. *Estuaries* 16: 809–814.

FETTEROLF, P.M. 1979. Nocturnal behaviour of Ring-billed Gulls during the early incubation period. *Canadian Journal of Zoology* 57: 1190–1195.

FOOTTIT, R.G. & BUTLER, R.W. 1977. Predation on nesting Glaucous-winged Gulls by River Otter. *Canadian Field-Naturalist* 91: 189–190.

GALUSHA, J.G. & HAYWARD, J.L. 2002. Bald Eagle activity at a gull colony and seal rookery on Protection Island, Washington. *Northwestern Naturalist* 83: 23–25.

GARTHE, S. & HÜPPOP, O. 1996. Nocturnal scavenging by gulls in the southern North Sea. *Colonial Waterbirds* 19: 232–241.

HAILMAN, J.P. 1964. The Galapagos Swallow-tailed Gull is nocturnal. *Wilson Bulletin* 76: 347–354.

HAYES, F.E., TURNER, D.G., ZIMMERLY, N.D. & PERALTA, M.B. 2018. Nocturnal courtship, copulation, and egg-laying in the Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*A. clarkii*). *Journal of Ethology* 36: 65–75.

HAYWARD, J.L. JR., AMLANER, C.J. JR., GILLET, W.H. & STOUT, J.F. 1975. Predation on nesting gulls by a River Otter in Washington State. *Murrelet* 6: 9–10.

HAYWARD, J.L., GALUSHA, J.G. & HENSON, S.M. 2010. Foraging-related activity of Bald Eagles at a Washington seabird colony and seal rookery. *Journal of Raptor Research* 44: 19–29.

HAYWARD, J.L., HENSON, S.M., BOVÉ, J., BOVÉ, C. & GREGORY, C.J. 2017. Daily and annual habitat use and habitat-to-habitat movement by Glaucous-winged Gulls at Protection Island, Washington. *Northwestern Naturalist* 98: 180–189.

HAYWARD, J.L. & VERBEEK, N.A. 2008. Glaucous-winged Gull (*Larus glaucescens*). In: POOLE, A. (Ed.). *Birds of North America Online*. Ithaca, USA: Cornell Laboratory of Ornithology. [Available online at: https://birdsna.org/Species-Account/bna/species/glwgul. Accessed 06 June 2019]. doi.org/10.2173/bna.59.

HÉBERT, P.N. & MCNEIL, R. 1999. Nocturnal activity of Ring-billed Gulls at and away from the colony. *Waterbirds* 22: 445–451.

HENSON, S.M., DENNIS, B., HAYWARD, J.L., CUSHING, J.M. & GLUSHA, J.G. 2007. Predicting the dynamics of animal behaviour in field populations. *Animal Behaviour* 74: 103–110.

HENSON, S.M., DESHARNAIS, R.A., FUNASAKI, E.T., GALUSHA, J.G., WATSON, J.W. & HAYWARD, J.L. 2019. Predator-prey dynamics of Bald Eagles and Glaucous-winged Gulls at Protection Island, Washington, USA. *Ecology and Evolution* 9: 3850–3867.

HENSON, S.M., WELDON, L.M, HAYWARD, J.L., GREENE, D.J., MEGNA, L.C. & SEREM, M.C. 2012. Coping behavior as an adaptation to stress: post-disturbance preening in colonial seabirds. *Journal of Biological Dynamics* 6: 17–37.

HOWELL, T.R., ARAYA, B. & MILLIE, W.R. 1974. Breeding biology of the Gray Gull. *University of California Publications in Zoology* 104: 1–57.

JAMES-VEITCH, E. & BOOTH, E.S. 1954. Behavior and life history of the Glaucous-winged Gull. *Walla Walla College Publications of the Department of Biological Sciences and the Biological Station* 12: 1–30.

JOHNSON, M., BECKMANN, J.P. & ORING, L.W. 2002. Temperate breeding shorebirds copulate at night. *Wader Study Group Bulletin* 97: 45–46.

JOHNSON, M., BECKMANN, J.P. & ORING, L.W. 2003. Diurnal and nocturnal behavior of breeding American Avocets. *Wilson Bulletin* 115: 176–185.

LA, V.T. 2011. Diurnal and nocturnal birds vocalize at night: a review. *The Condor* 114: 245–257.

LEOPOLD, F., PHILIPPART, C.J.M. & YORIO, P. 2010. Nocturnal feeding under artificial light conditions by Brown-hooded Gull (*Larus maculipennis*) in Puerto Madryn harbour (Chubut Province, Argentina). *El Hornero* 25: 55–60.

MARTIN, G. 1990. *Birds by Night*. London, UK: Poyser.

MARTIN, K.L.M. & RAIM, J.G. 2014. Avian predators target nocturnal runs of the beach-spawning marine fish, California Grunion, *Leuresthes tenuis* (Atherinopsidae). *Bulletin of the Southern California Academy of Science* 113: 187–199.

MCALLISTER, N.M. 1958. Courtship, hostile behavior, nest-establishment and egg laying in the Eared Grebe (*Podiceps caspicus*). *The Auk* 75: 290–311.

MCNEIL, R., DRAPEAU, P. & GOSS-CUSTARD, J.D. 1992. The occurrence and adaptive significance of nocturnal habits in waterfowl. *Biological Reviews* 67: 381–419.

MCNEIL, R., DRAPEAU, P. & PIEROTTI, R. 1993. Nocturnality in colonial waterbirds: occurrence, special adaptations, and suspected benefits. In: POWER, D.M. (Ed.). *Current Ornithology*. Vol. 10. New York, USA: Plenum Press, pp. 187–246.

MCWILLIAMS, K.M., SANDLER, A.G., ATKINS, G.J., HENSON, S.M. & HAYWARD, J.L. 2018. Courtship and copulation in Glaucous-winged Gulls, *Larus glaucescens*, and the influence of environmental variables. *Wilson Journal of Ornithology* 130: 270–285.

MEGNA, L.C., MONCRIEFF, A.E., HAYWARD, J.L. & HENSON, S.M. 2014. Equal reproductive success of phenotypes in the *Larus glaucescens-occidentalis* complex. *Journal of Avian Biology* 45: 410–416.

MONCRIEFF, A.E., MEGNA, L.C. & HAYWARD, J.L. 2013. Mating patterns and breeding success in gulls of the *Larus glaucescens-occidentalis* complex, Protection Island, Washington, USA. *Northwestern Naturalist* 94: 67–75.

MOYNIHAN, M. 1955. Some aspects of reproductive behavior in the Black-headed Gull (*Larus ridibundus ridibundus* L.) and related species. *Behaviour* Supplement 4: 1–201.

MOYNIHAN, M. 1962. Hostile and sexual behavior patterns of South American and Pacific Laridae. *Behaviour* Supplement 8: 1–365.

NELSON, D.A. 1989. Gull predation on Cassin's Auklet varies with the lunar cycle. *The Auk* 106: 495–497.

NEWTON, I. 2008. *The Migration Ecology of Birds*. London, UK: Academic Press.

NOCERA, J. & KRESS, S.W. 1996. Nocturnal predation on Common Terns by Great Black-backed Gulls. *Colonial Waterbirds* 19: 277–279.

ORO, J.D., RUIZ, X., JOVER, L., PEDROCCHI, V. & GONZÁLEZ-SOLÍS, J. 1997. Diet and adult time budgets of Audouin's Gull *Larus audouinii* in response to changes in commercial fisheries. *Ibis* 139: 631–637.

PUGH, A.R. & PAWSON, S.M. 2016. Artificial light at night potentially alters feeding behaviour of the native Southern Black-backed Gull (*Larus dominicanus*). *Notornis* 63: 37–39.

SALZER, D.W. & LARKIN, G.J. 1990. Impact of courtship feeding on clutch and third-egg size in Glaucous-winged Gulls. *Animal Behaviour* 39: 1149–1162.

SANDLER, A.G. 2013. *Features of Copulation and the Copulation Call in Glaucous-winged Gulls* (Larus glaucescens). MSc thesis. Berrien Springs, USA: Andrews University.

SOUTHERN, L.K. & SOUTHERN, W.E. 1979. Absence of nocturnal predator defense mechanisms in breeding gulls. *Proceedings of the Colonial Waterbird Group* 2: 157–162.

SOUTHERN, L.K., PATTON, S.R. & SOUTHERN, W.E. 1982. Nocturnal predation on *Larus* gulls. *Colonial Waterbirds* 5: 169–172.

TINBERGEN, N. 1959. Comparative studies of the behaviour of gulls (Laridae): a progress report. *Behaviour* 15: 1–70.

TINBERGEN, N. 1960. *The Herring Gull's World: A Study of the Social Behavior of Birds*. New York, USA: Harper & Row.

VERBEEK, A.M. & MORGAN, J.L. 1978. River Otter predation on Glaucous-winged Gulls on Mandarte Island, British Columbia. *Murrelet* 59: 92–95.

VERMEER, K. 1963. The breeding ecology of the Glaucous-winged Gull (*Larus glaucescens*) on Mandarte Island, B.C. *Occasional Papers of the British Columbia Provincial Museum* 13: 1–104.

YORIO, P., SUÁREZ, N., QUINTANA, F. & GATTO, A. 2005. Nocturnal activity in breeding Olrog's Gulls (*Larus atlanticus*). *Ornitología Neotropical* 16: 123–126.

ZAR, J.H. 2010. *Biostatistical Analysis, 5th Edition*. Upper Saddle River, USA: Pearson.