

# STREAKED SHEARWATER *Calonectris leucomelas* MOONLIGHT AVOIDANCE IN RESPONSE TO LOW AERIAL PREDATION PRESSURE, AND EFFECTS OF WIND SPEED AND DIRECTION ON COLONY ATTENDANCE

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## ABSTRACT

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Many species of Procellariidae are nocturnal on their breeding grounds, exhibiting reduced activity during fuller moonlight, perhaps to avoid predation by predators that use the full moon to hunt after sunset. Among these nocturnal species, Streaked Shearwaters *Calonectris leucomelas* have high wing loading and have difficulty taking off—especially with unfavorable wind conditions—thus potentially exacerbating moonlight avoidance. Effects of moonlight and wind conditions on the colony activity of this species, however, is poorly understood. We investigated the phenomenon by counting the departure and arrival of birds, and measuring ambient light intensity, local wind speed, and local wind direction at a breeding colony of Streaked Shearwaters on Awashima Island, Japan. Moon phase and ambient light had no significant effect on the frequency of arrivals or departures. Frequency of departures decreased significantly with increasing wind speed, but no effect was seen on arrivals, and wind direction had no effect on arrivals or departures. Our results indicate that: (1) wind speed may play an important role in Streaked Shearwater takeoff from the colony, and (2) moonlight avoidance is a plastic trait that may diminish in large-bodied shearwaters when few diurnal aerial predators are present.

**Key words:** moonlight avoidance, diurnal predators, wind conditions, colony attendance, Streaked Shearwater, *Calonectris leucomelas*, Sea of Japan

## INTRODUCTION

Procellariids and Hydrobatids are known to decrease colony attendance and reduce levels of vocalization in the colony under moonlight (Mougeot & Bretagnolle 2000, Rodríguez & Rodríguez 2009). Moonlight avoidance behavior may be a response to diurnal predators that use moonlight to hunt later into the night (Watanuki 1986, Mougeot & Bretagnolle 2000, Rubolini *et al.* 2014), and appears to influence landing, takeoff, and average return times on the breeding ground of these species (Keitt *et al.* 2004, Riou & Hamer 2008). Streaked Shearwaters *Calonectris leucomelas* are among those species thought to exhibit moonlight avoidance, but such behavior in this species has not been thoroughly studied. Their body mass (male: 569 ± 45 g, female: 489 ± 31 g; Yamamoto *et al.* 2016) is considered large among Procellariidae and Hydrobatidae genera, and it is thought that their large body size may reduce their predation risk by aerial predators compared to smaller petrels (Bretagnolle 1990b, Powell *et al.* 2008). Many procellariid species appear to be highly affected by moonlight, but there is evidence that larger species exhibit moonlight avoidance less frequently with low aerial predator abundance (Bretagnolle 1990b, Mougin *et al.* 2002, Powell *et al.* 2008). Indeed, Cory's Shearwaters *C. borealis*, a larger procellariid, decrease their activity at the colony under

moonlight when diurnal aerial predators are present, but not when these predators are absent (Granadeiro *et al.* 1998b, Mougin *et al.* 2002). This indicates that moonlight avoidance may be a plastic trait, particularly in larger species.

If moonlight avoidance is not the driving factor behind arrivals and departures, other factors may influence colony activity. Larger procellariids, including Streaked Shearwaters, have difficulty taking off from the ground or sea surface with no wind (Warham 1977). This is due to their relatively high wing loading (41.4 N/m<sup>2</sup>, Shirai *et al.* 2013) compared with gulls, terns, and smaller shearwaters (Warham 1977, Spear & Ainley 1997a, Hertel & Ballance 1999). To reduce takeoff costs, Streaked Shearwaters frequently leap from trees or steep banks to achieve enough lift for takeoff as they descend (Sato *et al.* 2009). Favorable wind speed and direction have also been demonstrated to aid takeoff and landing by generating more lift (Kogure *et al.* 2016). Favorable winds also appear to play an important role in shearwater travel, allowing for faster and more efficient commuting to and from foraging grounds (Weidinger 1996a, Spear & Ainley 1997a, Ross & Brunton 2002). This study aims to assess the extent of moonlight avoidance behavior of Streaked Shearwaters at a colony with low aerial predator pressure, and to test whether wind speed and direction affect colony attendance.

**METHODS**

**Study area**

This study was carried out 5–20 August 2017 on Awashima Island (38°28'N, 139°14'E; Niigata, Japan), during the Streaked Shearwater breeding season. Awashima is a small (9.86 km<sup>2</sup> total area), inhabited island located approximately 20 km from the mainland in the Sea of Japan. Awashima supports a large Streaked Shearwater colony, estimated at 80000 individuals (Yamamoto 2010). The northwest facing shearwater colony is located on the west coast of the island and is characterized by steep hills (up to 30°), and dense, low vegetation with few trees.

**Fieldwork procedures**

A 10 × 15 m portion of the colony that was directly illuminated on moonlit nights was chosen for the count. Counts were conducted once every night by 1–3 persons (most often 2–3), and birds were recorded departing from and arriving at the study plot for one 15-min count each night. Total colony activity was calculated as the sum of both arrivals to and departures from the colony. Counts occurred approximately 120 min after sunset to avoid potential confounding effects of changing sunset time and to ensure complete nightfall.

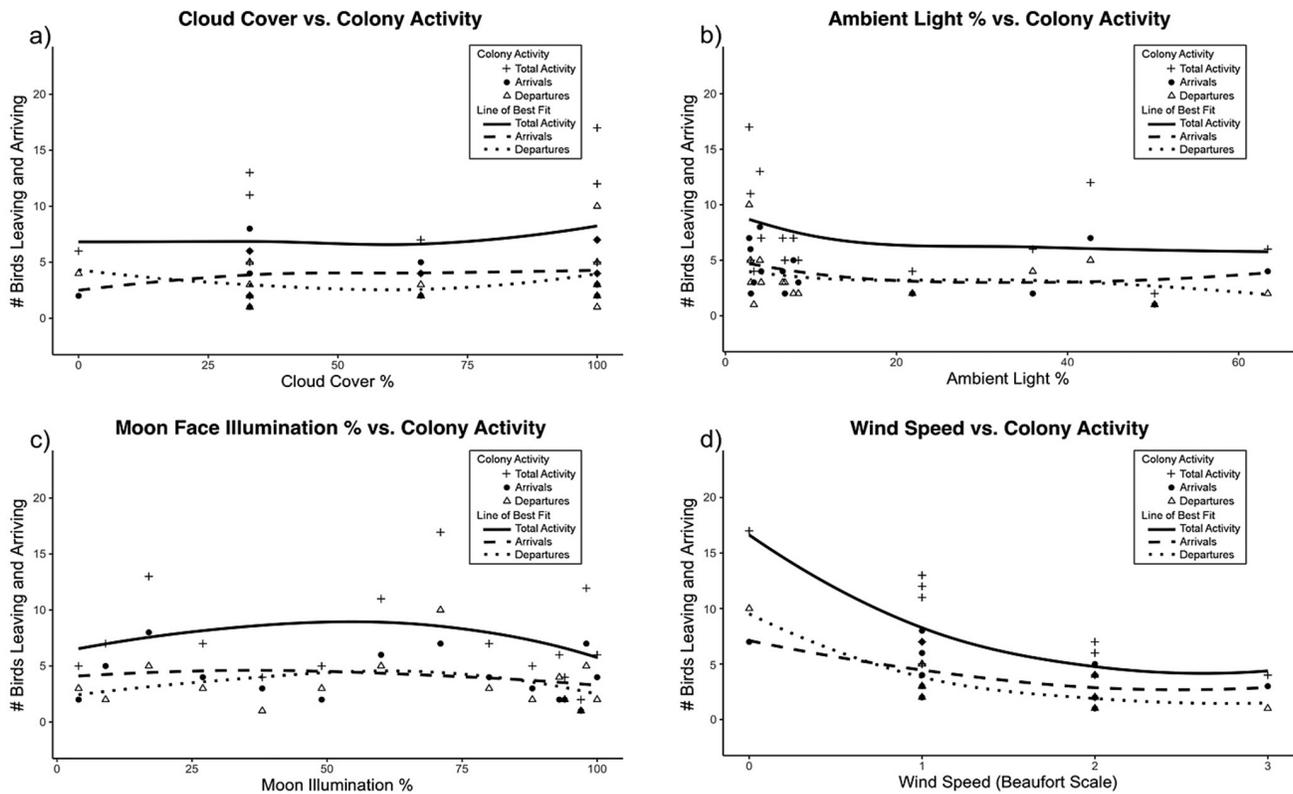
Counts on moonless or overcast nights were conducted in near darkness, so a Flir thermal scope and Vortex infrared night-vision

scope were used to enhance colony visibility for easier counting. Beaufort wind speed and cloud cover percentage (0 = clear, 1 ≈ 1/3 sky covered, 2 ≈ 2/3 sky covered, 3 = complete cloud cover) were recorded during each count. Due to equipment limitations, wind direction was not collected during counts, but was subsequently collected from the nearest local weather station (approximately 2 km from the colony) along with local wind speed before and after the counts. Hourly wind speed and direction were also collected from eight regional weather stations (approximately 35 km resolution, from stations 29–85 km away from the colony) for use in analyzing regional wind conditions and colony attendance patterns (see Appendix 1 for regional results and discussion).

Photographs, using a Canon EOS 600D RebelT3i with manually set ISO and shutter speed equipped with an 18-55 mm lens, were taken of the road surface near the colony, the colony, the sky over the colony, and the ocean opposite the colony immediately before or during the count. These photographs were analyzed for mean brightness as a measure of moonlight and ambient light intensity, when the moon was not present, using Gnu Image Manipulation Program (GIMP). Percentage of illuminated moon face was retrieved from <http://www.wunderground.com>.

**Statistical analyses**

All analyses (Table A1, Appendix 1) were performed in R (v3.4.2, R Core Development Team). All data were checked for normality and homoscedasticity. All statistical analyses were investigated



**Fig. 1.** (a) Non-significant environmental variables in relation to colony arrivals, (b) departures, and (c) total colony activity (total individuals arriving at and departing from colony); (d) wind speed over the study period (Beaufort Scale) in relation to colony arrivals, departures, and total colony activity over the study period.

using Generalized Linear Models (GLMs) (Poisson, log link; R base stats package v3.4.2), with circular variables transformed as sine and cosine. Model ranking was then undertaken to determine which models best described shearwater colony arrivals, departures, and total activity using Akaike’s Information Criterion for limited sample sizes (AICc, *MuMIn* package v1.40.0) for both linear and circular variables (Table 1).  $\Delta$ AICc and wAICc (*qpcR* package v1.4-0) were calculated to highlight the appropriateness of each

model. Models with the lowest AICc and coefficient confidence intervals not overlapping zero were chosen as the best models for each category where possible. Under-performing or overfitted models were removed from consideration for brevity.

Results are presented as mean  $\pm$  95% confidence interval. To decrease the likelihood of Type I errors due to the number of statistical tests conducted on the data set, the *p*-value significance

**TABLE 1**  
**Statistical values of the 10 most competitive models used to predict shearwater arrivals (A), departures (D), and total activity (T) at the Awashima colony**

	<b>Model</b>	<b>df</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b>wAICc</b>	<b>LR <math>\chi^2</math></b>	<b>P</b>
A1	AWS	2	54.9	0.0	0.445	3.18	0.128
A2	CC	2	56.4	1.6	0.203	1.61	0.810
A3	LL	2	57.8	2.9	0.102	3.30	0.675
A4	MP	2	58.1	3.2	0.091	0.25	0.765
A5	AWD	3	59.2	4.4	0.050	0.89	0.317
A6	MP + CC	3	59.9	5.0	0.036	1.20	0.632
A7	LL + CC	3	59.9	5.0	0.036	0.01	0.640
A8	LL + MP	3	61.1	6.2	0.020	1.19	0.663
A9	AWS + AWD	4	62.3	7.4	0.011	1.25	0.170
A10	LL + MP + CC	4	64.2	9.3	0.004	0.00	0.609
	<b>Model</b>	<b>df</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b>wAICc</b>	<b>LR <math>\chi^2</math></b>	<b>P</b>
D01	AWS	2	47.5	0.0	0.944	12.62	***
D02	AWS + AWD	4	54.3	6.8	0.031	9.30	***
D03	LL + MP	3	58.8	11.3	0.003	3.83	0.277
D04	LL	2	58.8	11.3	0.003	12.28	0.497
D05	AWD10	3	59.1	11.7	0.003	4.40	0.086
D06	AWS10 + AWD10	4	59.2	11.7	0.003	4.31	0.009
D07	CC	2	59.2	11.7	0.003	0.66	0.892
D08	AWD	3	59.3	11.8	0.003	8.34	0.163
D09	MP	2	59.8	12.3	0.002	1.01	0.999
D10	AWS11	2	59.9	12.4	0.002	8.46	0.947
	<b>Model</b>	<b>df</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b>wAICc</b>	<b>LR <math>\chi^2</math></b>	<b>P</b>
T01	AWS	2	59.6	0.0	0.967	14.61	***
T02	AWS + AWD	4	68.0	8.36352	0.015	8.29	***
T03	CC	2	71.4	11.72384	0.003	2.70	0.725
T04	AWD	3	71.6	11.94335	0.002	8.28	0.078
T05	LL + MP	3	72.3	12.67158	0.002	2.46	0.293
T06	LL	2	72.7	13.11036	0.001	13.13	0.349
T07	MP	2	74.1	14.42321	0.001	1.31	0.876
T08	MP + CC	3	74.3	14.66241	0.001	1.99	0.647
T09	LL + CC	3	74.8	15.13139	0.001	0.26	0.338
T10	LL + MP + CC	4	76.1	16.46324	0.000	2.91	0.292

<sup>a</sup> AWS: Awashima wind speed (during counts); AWD: Awashima wind direction (during counts); AWSn: Awashima wind speed (at n-pm); AWDn: Awashima wind direction (at n-pm); CC: cloud cover; LL: ambient light level; MP: moon phase

level was adjusted using the Bonferroni method and  $p$ -values were therefore considered significant at  $P < 0.0071$ .

## RESULTS

### Moonlight and cloud cover

During the study, we conducted 15 counts over a period of 16 d (a typhoon prevented data collection on one day), with a total of 60 colony arrivals and 51 colony departures recorded. Moon face illumination percentage (moon phase) decreased from 100% (7 August) to 4% (20 August) during the study period ( $61.67 \pm 17.74\%$ ). Moon phase had no significant effect on any measure of colony activity (arrivals, departures, total activity) (arriving:  $n = 15$ ,  $r = -0.1811$ ,  $P = 0.7653$ ; departing:  $r = 0.0081$ ,  $P = 0.9993$ ; total activity:  $r = -0.0922$ ,  $P = 0.8762$ ). Arrivals, departures, and total activity showed a downward trend as light levels increased, but the effects were not significant (arriving:  $n = 15$ ,  $r = -0.2132$ ,  $P = 0.6751$ ; departing:  $r = -0.2488$ ,  $P = 0.4972$ ; total activity:  $r = -0.2521$ ,  $P = 0.3488$ ) (Fig. 1a, b).

Cloud cover varied considerably ( $1.93 \pm 0.52$  cloud cover scale), and cloud cover showed no significant effect on arrivals, departures, or total colony activity (arriving:  $r = 0.1593$ ,  $P = 0.8098$ ; departing:  $r = 0.8917$ ,  $P = 0.6791$ ; total activity:  $r = 0.1428$ ,  $P = 0.7249$ ) (Fig. 1c). Both ambient light levels and cloud cover percentage scored high on the AICc table for all types of colony activity (Table 1), but neither model showed significant effects on colony activity (with the exception of ambient light versus total activity). Both were outcompeted by other models.

### Wind speed

Among the models proposed for arrivals, AICc calculations suggested local wind speed was the best predictor available (Table 1). Local wind speed models for departures and total activity also outperformed all other models in their respective categories, but complex models, including wind speed plus wind direction, or wind speed for multiple hours, could not be assessed with our dataset due to overfitting.

Increasing local wind speeds were correlated with fewer departures and total activity (arriving:  $r = -0.4911$ ,  $P = 0.1280$ ;

departing:  $r = -0.7459$ ,  $P = 0.0020$ ; total activity:  $r = -0.6769$ ,  $P = 0.0005$ ) (Fig. 1d; Fig. 2a, b, c). Local wind speed averaged Beaufort  $1.4 \pm 0.38$  (approximately  $3.57 \pm 0.96$  km/h) and did not reach over Beaufort 3 (19 km/h) during the study.

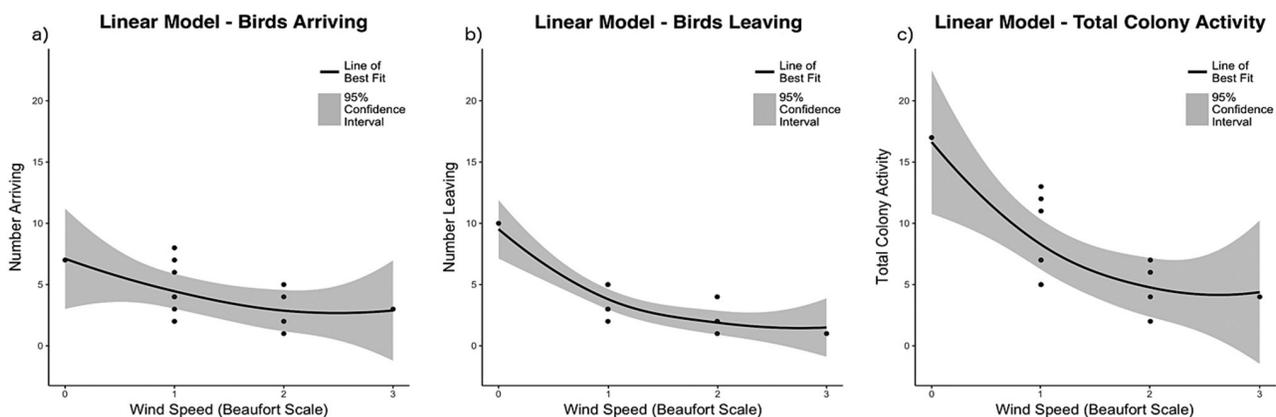
### Wind direction

We found no significant correlation between local wind direction and colony arrivals, departures, and total activity (arriving:  $r = 0.7766$ ,  $P = 0.3166$ ; departing:  $r = 0.8158$ ,  $P = 0.1627$ ; total activity:  $r = 0.7939$ ,  $P = 0.0783$ ). Local winds came most frequently from the northwest ( $315^\circ$ ), occurring during 40% of all counts. Mean local wind angle was  $312.67 \pm 24.34^\circ$ , or approximately WNW (Fig. 3). AICc calculations did not indicate that wind direction alone was a good predictor of any type of colony activity (Table 1). Interestingly, wind speed plus wind direction scored second highest on the AICc table, with a significant  $p$ -value for both departures and total activity, yet it performed poorly compared to the wind speed-only model (departing wAICc: AWS = 0.944, AWS + AWD = 0.031; total activity wAICc: AWS = 0.967, AWS + AWD = 0.015).

## DISCUSSION

### Moonlight avoidance

Moonlight avoidance is thought to be common in procellariid species (Mougeot & Bretagnolle 2000, Riou & Hamer 2008), but it may be a plastic trait, particularly for those of the *Calonectris* genus (Bretagnolle 1990, Granadeiro *et al.* 1998b, Rubolini *et al.* 2014). Our findings indicate that Streaked Shearwaters on Awashima do not avoid moonlight when arriving at and leaving from the colony. Lack of moonlight avoidance behavior has been observed in other procellariid species, including at Selvagem Grande, near the Canary Islands; the Poor Knights Islands and the Snares Islands, New Zealand; and South Plaza Island, Galapagos (Table 2). Adult Buller's Shearwaters *Ardenna bulleri* on the Poor Knights experience low levels of predation and appear to base their colony return on the sunset time (Harper 1983), not moonlight intensity, while species at the Selvagem Grande, Snares, and South Plaza colonies arrive before complete darkness and do not appear to be affected by nighttime ambient light levels (Snow 1965, Mougín *et al.* 2002). On South Plaza Island, Audubon's Shearwaters *Puffinus*

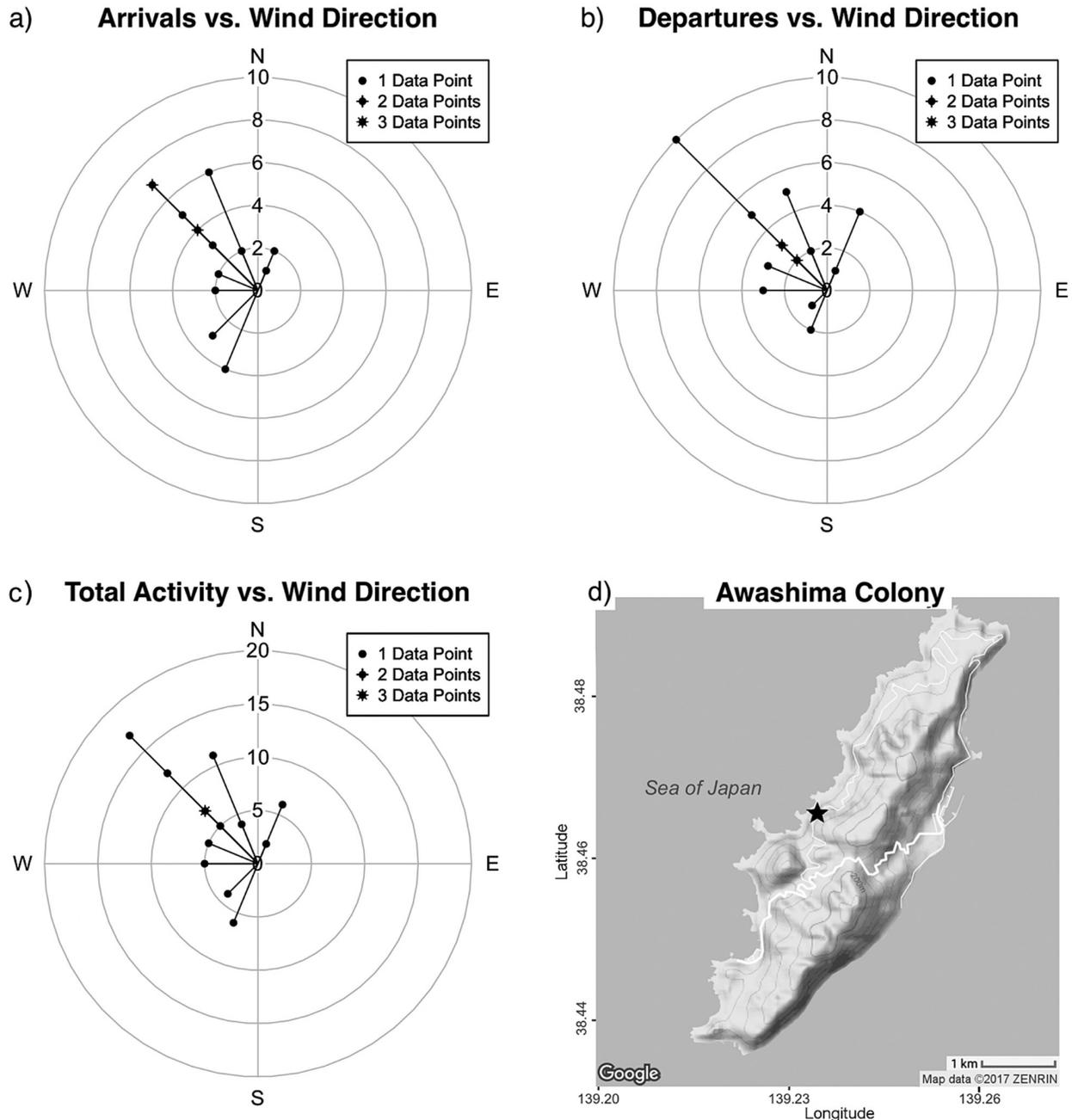


**Fig. 2.** Regression models and confidence intervals for (a) colony arrivals, (b) colony departures, and (c) total colony activity in relation to Beaufort wind speeds during the study period.

*lherminieri* have become diurnal to avoid predation by a nocturnal owl (Snow 1965), while their daytime colony activity at Selvagem Grande may be due, in part, to a lack of predators (Mougin *et al.* 2002). Snares Islands Sooty Shearwaters *A. grisea* are also active during the day (Richdale 1963), despite Brown Skuas *Stercorarius antarcticus*, an avid seabird predator, being present on the island. The reason for this behavior has not been identified, but it may also arise from low predation rates, as skuas are apt to take smaller and more diverse prey than Sooty Shearwaters (Young 1978). Small seabirds, including prions and storm petrels, are present in large numbers on the Snares Islands and provide an abundant source of

prey for skuas, so Sooty Shearwaters may not experience strong predation pressures from skuas.

The absence of moonlight avoidance by Streaked Shearwaters on Awashima is perhaps unsurprising. Aerial diurnal predators that take advantage of moonlight to hunt, including Large-billed Crows *Corvus macrorhynchos* and Slaty-backed Gulls *Larus schistisagus*, are present on Awashima, but predation pressure by these species appears to be low—no instances of these species feeding on adult shearwaters have been recorded. Feral cats *Felis catus* and Japanese Rat Snakes *Elaphe climacophora* are also



**Fig. 3.** (a) Colony arrivals, (b) departures, and (c) activity versus wind direction during count periods; (d) colony location on Awashima Island. Data points with modified symbols indicate two or more counts occurred with equal bird activity and wind direction. Wind direction expressed in graphs indicates wind source (i.e., line pointing due north indicates wind is blowing from north).

**TABLE 2**  
**Effects of ambient light on the activity of various procellariid species<sup>a</sup>**

Species	Colony Arrivals and Departures	Colony Return Time	Vocalization	Attraction to Artificial Lights	Life Stage Affected	Cause Cited	Reference
<i>Ardenna</i>							
<i>bulleri</i>		×			all adults	n/a	Harper 1983
<i>carneipes</i>	×	×			all adults	R	Powell <i>et al.</i> 2008
<i>grisea</i>	×	×	×		all adults	R	Richdale 1963
<i>Bulweria</i>							
<i>bulwerii</i>	–		–		non-breeding adults	P	Bretagnolle 1990b
				–	fledglings	P	Rodríguez & Rodríguez 2009
<i>Calonectris</i>							
<i>borealis</i>	×	×	×		all adults	n/a	Hamer & Read 1987
	×	×	×		all adults	n/a	Bretagnolle 1990b
	–				breeding adults	F	Klomp & Furness 1992
	×	×			n/a	R & F	Granadeiro <i>et al.</i> 1998b
	×	×			all adults	R	Mougin <i>et al.</i> 2002
				–	fledglings	P	Rodríguez & Rodríguez 2009
<i>diomedea</i>	–	–			breeding adults	P	Rubolini <i>et al.</i> 2014
<i>leucomelas</i>	×				all adults	R	This study
<i>Halobaena</i>							
<i>caerulea</i>	–		–		non-breeding adults	P	Mougeot & Bretagnolle 2000
<i>Oceanodroma</i>							
<i>castro</i>	–		–		non-breeding adults	P	Bretagnolle 1990b
<i>leucorhoa</i>	–				non-breeding adults	P	Watanuki 1986
<i>Pachyptila</i>							
<i>belcheri</i>	–		–		non-breeding adults	P	Mougeot & Bretagnolle 2000
		–			breeding adults	P	Silva & Granadeiro 2011
<i>turtur</i>	–				non-breeding adults	P	Richdale 1963
<i>vittata</i>	–				all adults	P	Richdale 1963

present on the island and have been documented to depredate shearwater chicks (Shiozaki *et al.* 2014). Adult predation by cats and snakes, however, is not limited to nighttime hours, and as a result these predators may not exert strong pressure on Streaked Shearwaters to remain nocturnal. While the total island population of feral cats on Awashima was estimated to be 70 individuals in 2015 (Yamamoto *et al.* 2016), Streaked Shearwaters' large body size may offer them some protection, as cats appear to prefer smaller prey (Van Aarde 1980, Van Rensburg 1985). Peregrine Falcons *Falco peregrinus* have been recorded preying on procellariids (White *et al.* 2002) and are present in small numbers on Awashima. Peregrines are known to hunt at night with the aid of urban lights (DeCandido & Allen 2006), but light pollution is minimal on Awashima and is significantly lower than light levels found in urban areas (Falchi *et al.* 2016). No shearwater carcasses depredated by Peregrine Falcons (plucked feathers and wings remaining) were found in the study area and surrounding areas, nor were any Peregrine Falcons detected hunting at night.

Although Peregrine Falcons are present, it is unlikely that they are a persistent source of nocturnal predation.

Larger procellariids are known to be less affected by moonlight than smaller species, possibly caused by reduced predation due to their larger body size (Bretagnolle 1990b, Powell *et al.* 2008). Bretagnolle (1990b) offers a weight cut-off for moonlight sensitivity at somewhere between the weight of Little Shearwaters *P. assimilis* (approx. 240 g; Onley & Scofield 2007) and Cory's Shearwaters (approx. 830g; Onley & Scofield 2007). Streaked Shearwaters are classified as large shearwaters (Onley & Scofield 2007), and typically weigh ~500 g (Onley & Scofield 2007, Yamamoto *et al.* 2016), putting them within the range of where procellariids appear to become less sensitive to moonlight. Large body size and low occurrence of diurnal aerial predators hunting with moonlight on Awashima may allow shearwaters to arrive at and depart from the colony without fear of predation under bright nocturnal conditions.

**TABLE 2 (continued)**  
**Effects of ambient light on the activity of various procellariid species<sup>a</sup>**

Species	Colony Arrivals and Departures	Colony Return Time	Vocalization	Attraction to Artificial Lights	Life Stage Affected	Cause Cited	Reference
<i>Pelagodroma</i>							
<i>marina</i>	–				non-breeding adults	P	Bretagnolle 1990b
<i>Pelecanoides</i>							
<i>urinatrix</i>		–			non-breeding adults	P	Mougeot & Bretagnolle 2000
<i>Pterodroma</i>							
<i>cookii</i>	–				all adults	F	Imber 1975
<i>gouldi</i>	–				all adults	F	Imber 1975
<i>Puffinus</i>							
<i>assimilis</i>	–	–			non-breeding adults	P	Bretagnolle 1990b
<i>auricularis</i>				–	fledglings	n/a	Telfer <i>et al.</i> 1987
<i>baroli</i>				–	fledglings	P	Rodríguez & Rodríguez 2009
<i>lherminieri</i>	×	×			all adults	P	Snow 1965
<i>opisthomelas</i>	–	–	–		all adults	P	Keitt <i>et al.</i> 2004
<i>puffinus</i>	–	–			breeding adults	P	Riou & Hamer 2008
					fledglings	P	Rodríguez & Rodríguez 2009
					fledglings	n/a	Syposz <i>et al.</i> 2018
<i>yelkouan</i>		–			all adults	P & F	Bourgeois <i>et al.</i> 2008

<sup>a</sup> ×, no effect; –, negative effect; blank space, no data/not studied; P, predator avoidance; R, reduced predation pressure; F, foraging efficiency; n/a, no explanation or multiple explanations given

**Wind speed**

Awashima colony activity and departures showed a significant negative correlation with increasing local wind speeds, while colony arrivals were negatively, but not significantly, correlated. Low wind speeds may increase colony arrivals because procellariids rely on high winds to forage and commute efficiently, and foraging becomes more energetically costly as wind speeds decrease (MacDonald 1980, Furness & Bryant 1996); high wind speeds may complicate landing maneuvers (Bourgeois *et al.* 2008, Mallory *et al.* 2009a). Because shearwaters experience high wing loading, they need momentum or wind to become airborne, and numerous bird species have been documented to use moderate to high winds to decrease the difficulty of taking off (Henderson & Kallok 2012, Kogure *et al.* 2016). Thus, it is surprising that fewer shearwaters left as winds increased. However, the bank where the Awashima colony is located may be steep enough that little to no wind may be needed for shearwaters to take off effectively, as numerous birds leap from the steep hillside in low wind conditions, much like individuals at other colonies who leap from trees to become airborne (Sato *et al.* 2009). Strong wind gusts may even complicate takeoff attempts, blowing birds off balance and deterring birds from departing from the colony (Mallory *et al.* 2009b). However, winds at the Awashima colony during this study reached up to 20 km/h (Beaufort 3), and it is unknown whether these low wind speeds would interfere with flight enough that shearwaters would be deterred from landing or taking off. Other factors may be influencing colony attendance, including prey availability (Klomp & Furness 1992), air temperature (Thayer *et al.* 1999), or other unstudied environmental effects.

**Wind direction**

Local wind direction was not significantly correlated with colony arrivals, departures, or total activity. The Awashima colony faces approximately NW (Fig. 3d), and winds originating from the NNW were most frequently observed during the study period, providing birds arriving at a 90° angle to the colony with tailwinds, and birds departing from the colony at 90° with headwinds. However, wind direction was measured at the nearest local weather station (1.82 km from colony), which was on the protected eastern side of Awashima. Therefore, conditions at the colony may have differed from those reported at the weather station.

Shearwaters and other procellariids are known to use wind directions to their advantage while commuting to reduce flight energy costs (Spear & Ainley 1997b, Weimerskirch *et al.* 2000, Tarroux *et al.* 2016). However, at the colony, wind direction appears to be less important. Frequency of colony arrivals was not significantly correlated with wind direction, perhaps because arriving shearwaters can orient themselves into the wind to decrease landing difficulty (Warham 1977), thus not being reliant on specific wind directions to land safely. Additionally, the low wind speeds during our study may not have been strong enough to cause wind direction to be a significant factor in shearwater arrival. Headwinds for departing birds significantly decrease the difficulty of taking off (Kogure *et al.* 2016), but again, with the low wind speeds typical of our study period, as well as the favorable terrain for taking off, wind direction may not have had a measurable impact on the difficulty experienced by Streaked Shearwaters at takeoff.

### Further Research

Our study shows that wind speed is a better predictor than moonlight intensity, wind direction, or cloud cover for Streaked Shearwater colony arrival and departure, but additional studies could further clarify these relationships. Our findings suggest that larger bodied shearwaters may not avoid moonlight at the colony, but little is known about whether age or breeding status influence moonlight avoidance. Studies of other procellariids suggest that breeding status and age may significantly affect moonlight sensitivity. Therefore, further assessment of the responses of breeding, non-breeding, and immature Streaked Shearwater to moonlight within the colony would be informative. Further studies on wind conditions with more sophisticated equipment (particularly localized wind speed and direction measurement equipment, and GPS units) are also warranted, as are studies of various other environmental factors—including at foraging grounds—to explore whether other factors influence the decisions of shearwaters to leave or return to the colony.

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