SEABIRD FLIGHT BEHAVIOR AND HEIGHT IN RESPONSE TO ALTERED WIND STRENGTH AND DIRECTION

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SUMMARY

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The ocean is swept by winds in regionally and seasonally predictable ways, and seabirds have been exploiting these patterns for millennia. Seabird use of wind energy is an under-appreciated aspect of seabird ecology. Using data from 114 cruises spanning the Southern Ocean, Peru Current, California Current and Equatorial Pacific from 1976 to 2006, we evaluate the effect of wind speed and direction on two key characteristics of seabird behavior, flight height and flight behavior. We used cluster analysis to partition 104 seabird species into morphological groupings based on degree of divergence in morphology from Pennycuick's "standard seabird," with subgroups evident among and within flappers, glide-flappers, and flap-gliders. Gliders, sea-anchor soarers and soarers showed no such divergence in morphology within their respective groups. Morphological grouping was in accord with foraging ecology, facilitating foraging behavior. Seabird flight height and behavior varied among groups and subgroups and changed as a function of wind speed and direction relative to travel, with the probability of more gliding and flying above 10 m increasing as wind speed increased. Most of the glide-flappers, flap-gliders and gliders, especially, would be highly vulnerable to offshore wind-generating facilities, as their flight heights bring them well within the blade-swept zone of typical turbines when winds are strong, and their more prevalent gliding makes them less maneuverable than flappers.

Key words: seabird flight behavior, flight height, offshore wind energy development

INTRODUCTION

Understanding the relationship between seabirds and wind has both ecological and practical application, being useful in further understanding resource partitioning (Pennycuick 1987, Spear & Ainley 1998), mobility (Pennycuick *et al.* 1984), and flight behavior as a clue to species' identities, as observed over a range of wind conditions in ocean-going surveys (e.g. Harrison 1983, Howell 2012). Flight behavior (i.e. prevalence of gliding, flapping, some combination of the two behaviors, and soaring) changes with wind speed for a given species (Pennycuick 1982, 2002). We can use this understanding to conduct fatality modeling for specific sites being evaluated for offshore wind energy development (e.g. Garthe & Hüppop 2004). Specifically, flight height information can be used to help predict potential impacts to seabird species from offshore wind farms, because flight heights >10 m would be within the rotor-sweep zone for most wind turbines — the typical turbine array used in Europe, where almost all research on seabird flight height has been conducted to date, has a propeller hub 70 m above the sea and a blade diameter of 100 m (Cook *et al*. 2012 and Johnston *et al*. 2013 use 20 m as the lowest flight height that would be a risk to seabirds). Given this context, the current paper provides evidence of seabird species' vulnerability by summarizing observed flight heights and behaviors and by modeling seabird flight height and behavior with respect to wind speed for several areas outside of Europe, although some species analyzed are found in Europe as well.

Ecological aspects of seabird flight

In a biophysical characterization, the way seabirds use or cope with the wind can be deduced by applying the laws of physics and aerodynamics (Pennycuick 1987a). Key properties of seabird morphology give clues to how a species will behave in long-distance flight; these properties are its mass (m), wing span (b), wing area (S) and disc area (the area of a circle with a diameter equal to the wing span). From these properties, *wing loading* (weight per unit wing area), *disc loading* (weight per disc unit area), and *wing aspect ratio* (length versus width) can be estimated. The *cross-sectional area* of the body (A) is also useful for evaluating capacity to use wind. As discussed in detail by Pennycuick (1987a), wing loading affects gliding speed and therefore the amount of flapping needed; disc loading affects the muscle power required for horizontal flight; wing length affects wing-beat frequency; and disc area and cross-sectional area affect the effective lift:drag ratio (Pennycuick 1987a).

The above properties and the derived properties (for example, mass and wing loading, respectively) can be combined to describe the flight capabilities of the "standard seabird," which resides midway in the geometric progression scaled to size among Procellariiformes, from storm-petrels (20 g) to the largest albatrosses (9 000 g; Pennycuick 1987a). Flight behavior of other species can be described by divergences from this progression, as a function of change in body mass, wing shape and size, wing length (aspect ratio or area remaining constant), and wing area (wing span remaining constant). Flight behavior also varies among species in accordance with aspects of foraging (for instance, prey size and mobility), and, thus, it may constitute an often-ignored element of niche separation (Pennycuick 1982, 1983, 1987b; Spear & Ainley 1998). Flight behavior also affects how far a species might range (Pennycuick 1982, 1987a), and what direction a bird may take in migrations or long-range movements (e.g. Spear & Ainley 1999, Adams & Flora 2010).

Flight behavior, the observed behavior at any given moment, is described by these terms: soaring, gliding, flap-gliding (more gliding than flapping), glide-flapping (more flapping than gliding), and flapping. Previous work has shown that flight behavior is affected by wind vector and that flight speed is affected by wind speed and direction (Spear & Ainley 1997 a, b). Flight style is a grouping of birds that most commonly exhibit certain flight behaviors. For example, a flapper (a style or group of birds) would generally undertake flapping flight, but may exhibit gliding behavior under certain conditions.

Flight behavior and flight height are related to variation in wind speed, as a seabird exploits the wind gradient, or wind boundary layer, over the ocean. Owing to surface friction, the wind speed over the ocean is significantly lower at its surface than it is about 10 m higher — most of the wind speed change occurs in the first 1–2 m above the ocean surface. Above 10 m, surface friction has little effect and wind speed changes are minimal with greater height (Bethwaite 2007). As an example of how the wind gradient affects flight, when flying into the wind, flappers would stay low to be in the zone where winds are lighter but, conversely, when flying with the wind, they would fly higher. Gliders and flap-gliders, in "gust soaring," use the wind gradient to maintain or increase flight speed — each rise above a wave crest is followed by banking and acceleration against the wind. The exceptions among seabird flight groups to the flight style progression (from flapping to flap-gliding to glide-flapping to gliding) are the true soaring flights of pelicans and frigatebirds (Pelecanidae, Fregatidae; Pennycuick 1983), and the sea-anchor flying of frigate and oceanitid storm-petrels (Hydrobatidae; Withers 1979).

Applied aspects of seabird flight

The demand for renewable energy is increasing worldwide. Since winds over the ocean are typically substantial and regionally and seasonally predictable, it is not surprising that over-ocean wind has become an increasingly more important part of the global renewable energy portfolio (e.g. Köller *et al*. 2006). Therefore, in addition to shipping and other industrial uses of the ocean, humans now plan to install wind-energy technology in the seabird realm.

Environmental effects of offshore wind-energy development are poorly known, as this human effort in coastal waters is new. Nevertheless, energy developers and resource agency staff will be required to quantify the effects. Consequently, in recent years, considerable progress has been made in understanding the nature of these effects (Köller *et al*. 2006, Drewitt & Langston 2006), particularly in regard to seabirds. Potential effects on seabirds include habitat loss and fragmentation due to avoidance of turbines, as well as increased injury or mortality due to collisions (e.g. Lapeña *et al.* 2010, Cook *et al.* 2012).

This paper provides information that can be used to help evaluate the potential risk of injury or mortality due to turbine collision, based on the relationships of flight height and flight behavior to wind speed. Models have been developed to predict possible effects on seabird groups as a function of flight height, but rarely is wind speed and how it affects flight height considered. This is due to constraints of data gathering: to ensure observer safety, data are rarely collected when winds are more than "moderate" (e.g., Garthe & Hüppop 2004, Johnston *et al*. 2013).

We analyze 30 years of data on flight behavior and flight height of 104 seabird species or species groups that were investigated on cruises in the Southern Ocean, Peru Current, California Current and Equatorial Pacific between 1976 and 2006. The data were not collected with any specific hypothesis in mind, other than for an eventual comparison of how seabirds use wind energy, but, since their collection, have been used to characterize seabird flight behavior (Spear & Ainley 1997a, b, 1998) and to correct estimates of seabird density (Spear *et al.* 1992, Clarke *et al.* 2003). We test *a posteriori* hypotheses developed to assess seabird flight height and wind speed: (1) groups of species are evident based on the degree to which they diverge in morphology from Pennycuick's "standard seabird;" (2) higher flight heights and changes in flight behavior are associated with increases in wind speed; and (3) species or species groups might be sorted by flight behavior in the same way that they might be sorted by bill size in their acquisition of food (e.g., Ashmole & Ashmole 1967). Foraging and flight behavior are closely linked and could be used to define niche space of a seabird species (Spear & Ainley 1998).

METHODS

Data collection

Data were obtained while conducting strip surveys to estimate seabird abundance at sea in five regions: (1) Antarctic/Southern Ocean, hereafter called the Antarctic (14 cruises; Ribic *et al.* 2011 for more details and cruise tracks), (2) Peru Current (17 cruises; Spear & Ainley 2007), (3) Panama Bight (12 cruises; Spear & Ainley 1999c), (4) California Current (59 cruises; Ainley *et al.* 2009, Ainley & Hyrenbach 2010), and (5) eastern Equatorial and subtropical Pacific, hereafter referred to as ETP (24 cruises, including Hawaii; Spear *et al.* 1999). The strip surveys occurred from 1976 to 2006 (Fig. 1). For this study, the data from the Panama Bight are included in those for the ETP, resulting in four regions.

During summer, surveys close to the coast could include a higher proportion of breeding and therefore commuting birds, which could affect their flight behavior. That is, commuting birds would fly into the wind more than they would normally, depending on where their colony is located relative to where the birds are encountered and relative to the wind direction. In that regard, the majority of cruise

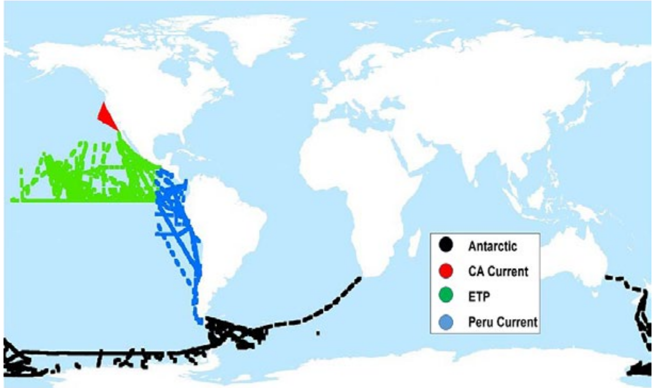

Fig. 1. Location of cruise tracks for seabird strip surveys from 1976 to 2006.

points (58%) were >50 km from shore, although the percentage varied by location: 25% of the cruise points in the California Current were collected at points >50 km from shore, compared with 74% for the Antarctic, 99% for the EPT, and 78% for the Peru Current.

Once underway, two bird monitors aided by binoculars searched one forequarter on the side with least glare, out to 300 m on most cruises, or to 600 m in equatorial/subtropical waters where larger ships offered greater height above the sea surface and ocean waves were generally lower (see Spear *et al*. 1992, 2004 for further details). All vessels were ocean-going, at least 50 m in length, and underway in all conditions, although we rarely collected data when winds were >18 m/s (>35 knots). Each seabird sighting included species identification, direction of travel and behavior (sitting on surface, flapping, flap-gliding or glide-flapping, and gliding). We did not include sightings during which birds were foraging, milling around a food source, flying to a known food source, or attracted to or following the ship. We estimated flight height by comparing our height above the sea surface (generally 12–25 m) with the bird's height, or by comparing the bird's wing span (see Pennycuick 2002 for a similar approach) or by both methods. Height was recorded in three categories: <3 m, 3–10 m and >10 m.

Wind speed and direction were determined from the ship's anemometers, which were placed on the instrument mast at least 20 m above the sea surface. We adjusted wind speeds according to the prospective wind gradient. We designated flight direction (i.e. headwinds, crosswinds, or tailwinds) for birds based on Spear & Ainley (1997a, b), and added a categorical version of wind speed, using the following six categories: <5.1 m/s (<18.4 km/h), 5.1–7.7 m/s (18.4–27.7 km/h), 7.7–10.3 m/s (27.7–37.1 km/h), 10.3–12.9 m/s (37.1–46.4 km/h), 12.9–15.4 m/s (46.4–55.4 km/h) and ≥15.4 m/s (>55.4 km/h).

Data analysis

We defined our database to include a reasoned selection of seabird species. The original seabird strip survey database included over 250 species, but we narrowed the list to those 104 species having at least 20 observations within groupings relative to major wind directions, i.e., headwind, crosswind or tailwind.

We conducted cluster analyses of seabird morphology measurements to define morphological clusters of seabird species. The analyses were conducted on morphological data (i.e. wing span, loading, aspect, wing area and mass), as summarized in Spear & Ainley (1997a), which were obtained by direct measurement of specimens as well as from the literature. We used a partitioning approach to subdivide the flight styles of flappers, glide-flappers, and flap-gliders into morphological groups (referred to hereafter as "clusters;" Table 1). We did not include gliders (small albatrosses and large gadfly petrels), soarers (pelicans and frigatebirds), and sea-anchor soarers (frigate and oceanitid storm-petrels) in the cluster analyses because the morphology of species within these flight styles was homogeneous and the samples of these species were small.

TABLE 1
First two principal components in the clustering analyses, and strongest associations with morphological attributes

Flight style	First principal component	Second principal component
Flappers	Wing loading, $r = -0.922$	Wing span, $r = 0.900$
Glide-flappers	Wing span, $r = 0.889$	Aspect ratio, $r = 0.935$
Flap-gliders	Wing span, $r = 0.747$	Wing loading, $r = -0.807$

We looked at correlations in the dataset to eliminate redundant morphological variables; those such as wing area and mass were eliminated in this step, leaving wing span, loading, and aspect ratio as the variables for the cluster analysis. We used R software (R Development Core Team 2012) to conduct the analyses, and employed the "cluster" package (Maechler 2012). The function "pam" allowed us to assess the most efficient numbers of clusters based on (1) the average dissimilarity between observations within a cluster, and (2) the dissimilarity between observations and their nearest neighbor cluster. We plotted clustering results for the two best clustering options based on these criteria, using the R functions "clara" and "clusplot." Approximately one-third of the seabird species (30 of the 104 species analyzed) did not have associated morphological data, so we assigned them to newly defined clusters based on professional judgment. That is, we based an assignment on known morphological similarities to other species. For example, members of the "Manx shearwater" group were clustered together, although they have long since been divided into separate species. These designations were also used in subsequent modeling.

In order to evaluate the effect of wind speed on flight height, we used generalized linear mixed models, with morphological group as the random variable. We chose a mixed model approach because of the lack of independence within a group as well as our interest in extending inference beyond the species sampled here to seabirds more generally (Faraway 2006). Our response variable was a binary term representing flying below 10 m or above 10 m, in part because of the way the data were collected (by height category). The fixed predictor variables included location (Antarctic, California Current, ETP, or Peru Current), wind speed (m/s), relative wind direction (headwind, crosswind, tailwind), and the interaction between wind speed and relative wind direction. Following Zuur *et al.* (2009) and Bolker *et al.* (2009), we first identified the best random structure by comparing three models using likelihood ratio tests: the models were identical with respect to the fixed terms (each contained the full set of fixed terms), but they differed in their random structure, with the first model containing morphological group as a random intercept, the second containing morphological group as a random slope, and the third model containing morphological group as a random slope and intercept. Based on these tests, we used a random intercept and slope in all candidate models moving forward. Once the random structure was identified, we evaluated the contribution of the fixed effects using an information theoretic approach. We calculated Akaike information criteria corrected for small sample sizes (AICc), including values and weights of 10 candidate models, and calculated evidence ratios for the two models with the lowest AICc scores. We did not model-average because the model with the lowest AICc value had a weight of 1. Mixed models were fit by maximum likelihood using Laplace approximation in the lme4 library in R (Bates *et al*. 2014, R Core Team 2014).

We used linear regression analysis to evaluate the effect of wind speed on flight behavior. We divided flying behavior into five categories that typically characterize a species: (1) flapping, (2) flapping, few glides, (3) flap-gliding, (4) gliding, few flaps, and (5) gliding. We were interested in how wind speed might affect a species' typical behavior, e.g. at what wind speed would a gull transition from mostly flapping to exercise more gliding (flapper to flap-glider)? For each group, we scaled the number of birds exhibiting each behavior by the number of birds observed in each wind category. We then evaluated the change in proportion as a function of wind speed category. We tested for statistical significance of a linear trend in behavior as a function of wind speed using *t*-tests at a significance level of 0.05.

Interpretation of modeling results

The practical application of these data and models is to identify seabird clusters that are most vulnerable to being in the rotor-swept zone of typical offshore wind turbines currently used and to flying in a way that decreases maneuverability (i.e. >10 m high and mostly gliding). Therefore, we wanted to interpret the results of our flight

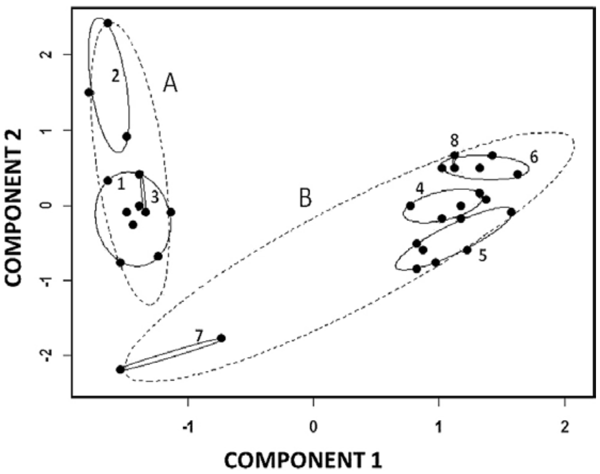

Fig. 2. Cluster analysis of flappers: 1, small alcids and diving petrels; 2, large alcids and loons; 3, cormorants; 4, medium gulls; 5, terns; 6, large gulls; 7, phalaropes; 8, tropicbirds. See Appendix 1, available on the Web site, for a complete list of species in each cluster.

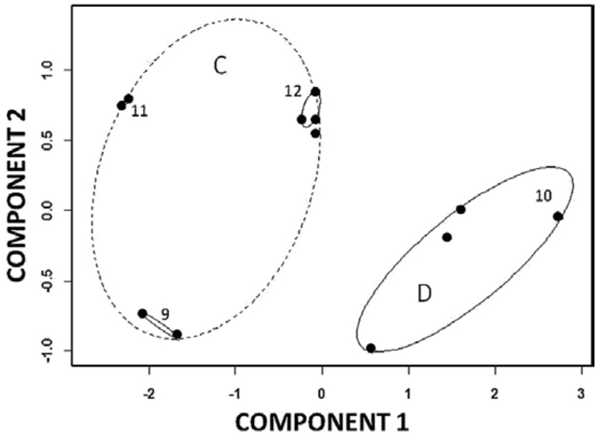

Fig. 3. Cluster analysis results for glide-flappers: cluster 9, boobies; cluster 10, small petrels and storm-petrels; cluster 11, pelicans; and cluster 12, large skuas. See Appendix 1, available on the Web site, for a complete list of species in each cluster.

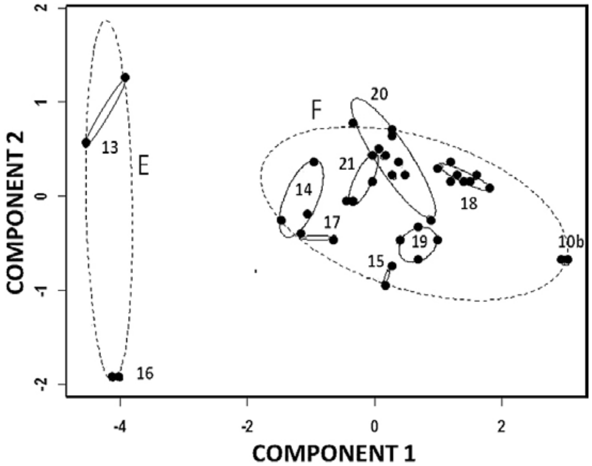

Fig. 4. Cluster analysis results for flap-gliders: 13, small albatross; 14, long-ranging boobies and *Procellaria*; 15, fulmars; 16, giant fulmars; 17, large aquatic shearwaters; 18, small gadflys; 19, small aquatic shearwaters; 20, large gadflys; 21, medium gadflys and large aquatic shearwaters. See Appendix 1, available on the Web site, for a complete list of species in each cluster. Note that Cluster 10b appeared to be an outlier but, upon inspection of modeling results, it was placed among the glide-flappers (and with Cluster 10, Fig. 3).

TABLE 2
Effect of wind speed on flight height: 10 candidate models showing AICc values and weights[a]

Fixed Predictors	Modnames	K	AICc	ΔAICc	AICcWt	LL
Wind + RelDir + Location + Wind*RelDir	m1	12	34 321.50	0	1	-17 148.7
Wind + RelDir + Location	m2	10	34 463.77	142.277	0	-17 221.9
RelDir + Location	m6	9	34 486.19	164.694	0	-17 234.1
1 [null model]	m10	4	39 091.66	4 770.162	0	-19 541.8
Location	m9	7	35 832.82	1 511.319	0	-17 909.4
RelDir	m8	6	37 914.43	3 592.929	0	-18 951.2
Wind	m7	5	39 088.01	4 766.514	0	-19 539.0
Wind + Location	m5	8	35 825.11	1 503.610	0	-17 904.6
Wind + RelDir	m4	7	37 901.84	3 580.344	0	-18 943.9
Wind + RelDir + Wind*RelDir	m3	9	37 799.9	3 478.404	0	-18 890.9

[a] All models had the same random predictor (cluster group [intercept and slope]) and cumulative weight (= 1); among fixed predictors, RelDir = relative direction (bird vs. wind). AICc = corrected (for sample size) Akaike's information criterion; Modnames = model names, using a number for convenience; K = number of estimated parameters; **ΔAICc** = difference in AICc of present model to the model with the lowest AIC score (m1); AICcWt = AICc weight; and LL = Log Likelihood.

TABLE 3
Summary of parameter estimates of fixed effects of the best model

Parameter	Estimate	Standard error	z value	Pr (>|z|)
(Intercept)	-1.5120	0.6057	-2.5	0.0125
Wind speed	0.1794	0.0187	9.58	$< 2 \times 10^{-16}$
Headwind	-0.7670	0.0593	-12.94	$< 2 \times 10^{-16}$
Tailwind	-0.3481	0.0605	-5.75	8.80×10^{-9}
California Current	-1.6391	0.0543	-30.17	$< 2 \times 10^{-16}$
ETP	-3.2725	0.0739	-44.26	$< 2 \times 10^{-16}$
Peru Current	-3.1522	0.0875	-36.04	$< 2 \times 10^{-16}$
Wind speed:Headwind	-0.1049	0.0115	-9.11	$< 2 \times 10^{-16}$
Wind speed:Tailwind	-0.0099	0.0114	-0.87	0.3831

height analysis to make statements about how these factors might contribute to the vulnerability of seabirds to offshore wind turbines. Conservatively, we defined vulnerability to flying within the rotor-swept zone if the probability of flying at a height >10 m is greater than 0.5. We plotted predicted flight heights as a function of wind speed for each geographical region, and identified the wind speeds at which the predicted probability of flying above 10 m is >0.5. We also performed a qualitative assessment of the relative vulnerability of morphological clusters by comparing slopes of the random effects; however, formal between-group comparisons are not appropriate for levels within a random effect. For a given flight style (but increasing with the amount of gliding), we identified which clusters are vulnerable over the range of any of the observed wind speeds for any of the flight directions. For the vulnerable clusters, we determined the wind speeds and flight directions at which they are vulnerable.

TABLE 4
Generalized linear mixed model analysis of flight height and wind speed with the random effect morphology/flight style groups ranked lowest to highest by degree of slope

Group	Intercept	Slope	Antarctic, n	California current, n	ETP, n	Peru current, n
Large gulls	3.255189	-0.06581	88	6 335	0	0
Small gulls	2.854298	-0.06572	0	393	0	55
Skuas	3.03459	-0.06148	216	480	305	302
Phalaropes	-0.50362	-0.05618	0	1 129	144	158
Oceanites	-3.47945	-0.04602	734	0	0	741
Medium-sized gulls	3.236653	-0.0427	0	2 126	0	213
Cormorants	-0.07102	-0.03735	0	959	0	27
Frigate petrels	-3.01924	-0.03717	309	0	21	804
Oceanodroma	-4.67778	-0.03021	0	3 279	6470	3 588
Tropicbirds	5.115913	-0.01523	0	0	28	0
Small alcids	-3.73632	-0.01516	206	1 125	0	0
Frigatebird	7.795711	-0.00994	0	0	0	30
Small albatrosses	0.052342	-0.00796	153	1 109	0	225
Large gadfly petrels	-1.43934	-0.00711	164	0	4 299	1 163
Medium-sized alcids	-2.53977	-0.00168	0	595	0	0
Prions	-1.0231	-0.00121	3 046	0	0	78
Manx-type shearwaters	-4.07447	0.000922	35	113	386	71
Pelicans	2.038491	0.00166	0	334	0	325
Loon grebe	1.029396	0.007822	0	254	0	0
Giant petrels	-0.96771	0.018279	99	0	0	0
Small gadfly petrels	-0.176	0.018574	3 748	137	3 647	884
Surface-feeding shearwaters	-1.18405	0.036555	345	1 673	2 350	566
Boobies	2.240037	0.040926	0	0	329	1 136
Fulmars	-1.02046	0.060311	1 278	1 633	0	139
Large alcids	-2.03463	0.087591	0	5 933	0	0
Terns	2.119291	0.09448	490	211	1 802	151
Diving shearwaters	-1.27113	0.142368	2 728	10 991	886	543

RESULTS

Cluster analysis based on morphology

We used the cluster analysis to subdivide flappers, glide-flappers, and flap-gliders into two coarser clusters (indicated by letter) and numerous finer-scaled clusters (indicated by numbers) (Figs. 2–4, Appendix 1 available on the Web site). The coarse scale clustering revealed two major groups for each of the flight styles (A&B, C&D, E&F). The finer-scaled clustering revealed two to eight clusters within the coarse scale groups. A complete list of all species, as divided into these clusters, is presented in Appendix 1 (available on the Web site), including those that were part of the analysis and those that were not (i.e. those that were classified based on known morphological similarities to clustered species; see Methods). The fine-scale cluster results allowed us to proceed with the initial modeling runs to investigate flight behavior and height as a function of wind speed and flight direction.

Flight height

The full model, composed of location, wind speed, relative wind direction and the interaction between relative wind direction and wind speed, as well as a random intercept and slope for morphological groups, resulted in the best-supported model, with an AIC weight of 1 (Table 2). The ΔAICc between this and the second-best model (without the fixed interaction term) is 142. The evidence ratio between the top two models is 2.893032×10^{30}. Table 3 shows the fixed effects used in the modeling.

The slopes and intercepts for the random effects related to flight height are consistent with flight styles and morphological groups, and particularly with wing loading (Table 4, Fig. 5). Those groups with high wing loading and the diving shearwaters (Procellariidae), in particular – see Kuroda (1954) for separation of diving from surface-feeding shearwaters – flew higher as wind speed increased. Other groups with high wing loading that tend to fly by flapping, specifically terns (Sternidae) and large alcids (Alcidae), ranked next. However, these groups may not have been strictly comparable to the shearwaters, because they were commuting between breeding and feeding grounds (as indicated by their location) and were coping with high winds rather than using them (see Discussion). The next highest-ranked groups, fulmars (Procellariidae), boobies (Sulidae, especially long-distance species) and surface-feeding shearwaters (Procellariidae), also tended to fly especially high as winds increased. The groups of lowest rank were all flappers, e.g. gulls (Laridae), skuas (Stercorariidae), phalaropes (Scolopacidae), storm-petrels, tropicbirds (Phaethontidae), cormorants (Phalacrocoracidae) and small alcids (Alcidae), and tended to fly lower with stronger winds. Many have a small body size. The large gulls and cormorants, almost all sampled in the California Current, were commuting.

With respect to region, seabirds on the whole tended to reach higher heights with stronger winds in the Southern Ocean and to a lesser extent the California Current (Fig. 6). Height increased at lower wind speeds in those areas, as well, compared with heights achieved at those wind speeds in the ETP and Peru Current regions. In the higher wind speed categories, the confidence intervals around the regression coefficients broadened with stronger winds, likely reflecting the differing responses of flight groups.

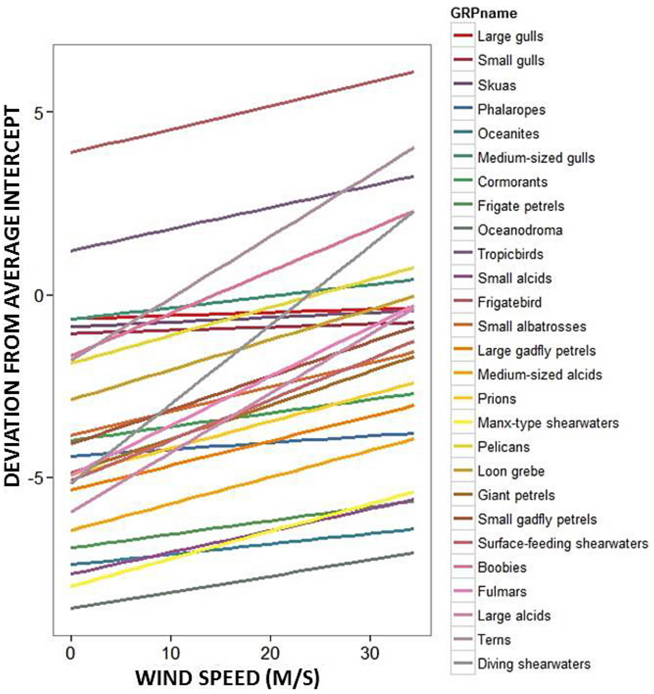

Fig. 5. Slopes and intercepts for the random effect in the relationship between flight height and wind speed compared among morphological groups.

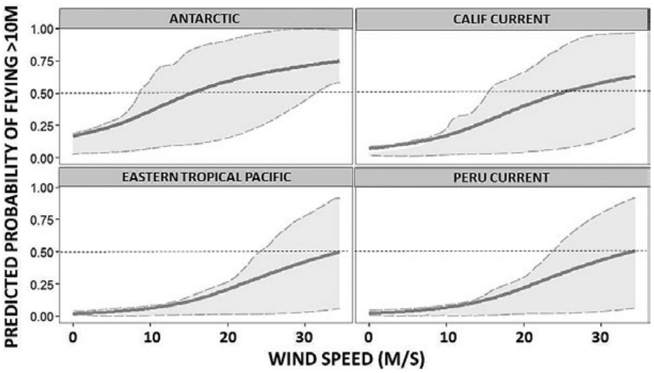

Fig. 6. Model predictions (with upper and lower quartiles) of the probability of seabirds flying higher than 10 m as a function of wind speed. Each region includes all species groups found in that region.

TABLE 5
Proportion seen flapping or gliding by flight style

Flight style	Proportion seen flapping	Proportion seen gliding
Flappers	0.71 to 0.92	0.01 to 0.10
Glide-flappers	0.14 to 0.44	0.02 to 0.15
Flap-gliders	0.03 to 0.12	0.21 to 0.53
Gliders	0.00 to 0.09	0.73 to 1.00
Sea-anchor soarers	0.14 to 0.45	0.00 to 0.21

Flight behavior

For the most part, species that are flappers showed an increase in prevalence of flapping with increasing wind: loons/grebes, cormorants, large and medium alcids, large and small gulls (but not medium-sized gulls), terns, and tropicbirds (Tables 5, 6). Glide-flappers, such as pelicans and boobies, showed this tendency as well. Flap-gliders, such as diving and surface-feeding shearwaters, small and large gadfly petrels (Procellariidae), small albatrosses (Diomedeidae), giant petrels (Procellariidae) and fulmars, exhibited an increase in the preponderance of gliding with higher wind speeds. *Oceanodroma* storm-petrels exhibited slightly increased glides with stronger winds but *Oceanites* storm-petrels did not. A number of species, such as the latter, frigatebirds, phalaropes, prions (Procellariidae), and perhaps small alcids, showed little change in flight style with increased wind speed.

DISCUSSION

Clustering

Morphology is often greatly confounded by phylogeny, and a quick glance at our modeling results shows a strong influence of phylogeny. However, what we find interesting is that our clustering was based on morphology related directly to flight capability, which is almost never measured by seabird researchers, who are quite familiar nevertheless with wing chord, tail, tarsus and bill length (e.g. Brooke 2004). While we did not intend to compare our results with a phylogenetic species array, it is clear that many closely related species use or cope with the wind similarly, but so do some not-so-closely related species. In general, changing the morphology of Pennycuick's (1987a) "standard seabird" produces the diversification of flight styles and capabilities shown in our

TABLE 6
Results of regression analyses of change in flight style with increasing wind speed[a]

	Flapping	Flap, few glides	Flap-gliding	Glide, few flaps	Gliding
Boobies	+	NS	-	NS	NS
Cormorants	+	NS	NS	-	NS
Diving shearwaters	NS	NS	-	-	+
Frigate petrels	NS	NS	-	NS	NS
Frigatebird	NS	NS	NS	NS	NS
Fulmars	+	NS	-	NS	+
Giant petrels	NS	NS	-	NA	+
Large alcids	+	NS	NS	-	NS
Large gadfly petrels	NS	NS	NS	-	+
Large gulls	+	-	NS	NS	NS
Loon/grebe	+	NS	NS	-	NS
Manx-type shearwaters	NS	-	+	-	NS
Medium-sized alcids	+	NS	NS	-	NS
Medium-sized gulls	-	NS	NS	NS	NS
Oceanites	NS	NS	NS	NS	NS
Oceanodroma	-	+	NS	NS	NS
Pelicans	+	NS	NS	NS	NS
Phalaropes	NS	NS	NS	NS	NS
Prions	NS	NS	NS	NS	NS
Skuas	NS	-	NS	NS	NS
Small albatrosses	NS	NS	-	-	+
Small alcids	NS	+	NS	NS	NS
Small gadfly petrels	NS	NS	-	NS	+
Small gulls	+	-	NS	NS	NS
Surface-feeding shearwaters	NS	NS	-	NS	+
Terns	+	NS	-	NS	-
Tropicbirds	+	NS	-	NS	NS

[a] A positive symbol indicates a significant positive relationship (e.g. more flapping with increased wind) and a negative symbol indicates the opposite (NS indicates no significant relationship).

cluster analysis. In a variation on Pennycuick's discussion, at the coarse scale of clustering (the lettered groups A&B, C&D and E&F) and staying close to the standard, our clustering reveals the flap-gliders have a range of body sizes (Fig. 4). Much of the clustering at this level has to do with phylogeny. Increasing wing length and aspect ratio from the "standard seabird" produces the gliders; shortening the wings and increasing wing loading results in the flappers (Fig. 2). Lengthening the wings without changing aspect ratio but reducing wing loading results in the soarers (frigatebirds); broadening the wings results in the glide-flappers (Fig. 3); and adding long legs and large feet results in the sea-anchor soarers (frigate and oceanitid storm-petrels).

Considering the flight-speed groupings of Spear & Ainley (1997b; Appendix 1 available on the Web site) allows us to understand the array of finer-scale clusters (numbered groups). Relative flight speed and the morphological characteristics that affect speed appear to play a role in seabird wind energy use. This is indicated in part by the fact that a number of species with high aspect ratios remain on the water when there is no wind (data not shown). While the soarers ride thermals, seabirds without the lift provided by thermals need to maintain air speed or take advantage of higher wind speed for effective flight. Thus, slight variations among close-to-the-standard flap-gliders (Fig. 4) separate small albatross and giant fulmars (Clusters 13 and 16) that need faster flight speed because of their increased wing loading (flight speed groups 1 and 3) from the remaining seven clusters of flap-gliders (not including Cluster 10b), i.e. various petrels plus long-ranging boobies (see flight speed groups 2, 4 to 9, some of 15). Coarse-scale clustering of the glide-flappers separated slow-flying small petrels/aerial storm-petrels (flight speed groups 6, 12) from heavier, faster-flying boobies, pelicans and large skuas (flight speed groups 14, 15, 17). Finally, all the flappers can be found among flight speed groups 16 and 18–25. Among these clusters, as wings become smaller and more adapted to underwater flight, aerial flight speed (and wing-beat frequency) needs to become faster for them to stay aloft and make horizontal progress. Thus, the heavy-body, high wing-loading, diving species (flight speed groups 22–25) are separated from the non-diving flappers (flight speed groups 13, 16 [small skuas], 18–21).

There were some anomalous groupings in the clustering (Appendix 1 available on the Web site). For instance, Franklin's Gull was grouped with terns (coarse and fine Cluster B-5) but seemingly should have been grouped with medium gulls (Cluster B-4); Short-tailed Shearwater was grouped with somewhat divergent small gadfly petrels (Cluster F-21) but seemingly should have been grouped with large aquatic shearwaters (Cluster F-17). The explanation for these anomalies is likely to do with sample size. In the specimens or published measurements available to Spear & Ainley (1997a), there was only one Franklin's Gull, and thus the measurements may not have been representative of the species. Likewise, there were only two Mottled Petrels and three Kerguelen Petrels in the sample, and, given they were measured during winter and in some stage of wing molt, their wings were shaped more like those of the similar-sized, aquatic Short-tailed Shearwater. Not including the two petrels, the Short-tailed Shearwater would have been clustered with the other aquatic shearwaters (Cluster 17). On the other hand, since its sample sizes seemed adequate, why the Leach's Storm-Petrel (Cluster 10b) was not grouped with the other *Oceanodroma* storm-petrels is perplexing. The other *Oceanodroma* storm-petrels have far narrower ranges than the Leach's. The latter breeds at high latitudes but winters in the tropics, whereas the other *Oceanodroma* measured are found in the same general respective regions year-round. Thus, in fact, the clustering may have identified a real difference: longer wings for the Leach's Storm-Petrel. Power & Ainley (1986) found that Leach's Storm-Petrel populations that nest farther from the tropics (where they wintered) had longer, thinner wings than those nesting closer to breeding areas, a pattern similar to migratory land birds and consistent with wing shape and ranging behavior in other seabirds (Pennycuick 1987a). Finally, we placed Hornby's Storm-Petrel among the sea-anchor soarers on the basis of our observations and the fact that their legs are longer and feet larger than other *Oceanodroma*; it is possible that investigation of this little-known species would reveal that it is not of that genus.

Flight height and behavior

When we began to log flight height and behavior during our at-sea cruises, we put observations into one of four height categories: <1 m, 1–3 m, 3–10 m, >10 m, but we now believe we should have estimated actual height for each bird sighting. Once we experienced the full range of wind conditions that can be encountered, even hurricane-force winds, it became clear that in winds >18 m/s (>35 knots), many seabirds attain heights far greater than 10 m, e.g. to 50 m or more. Thus, our range of categories has resulted in an understatement with respect to height, especially among gliders and flap-gliders, and to a lesser degree among glide-flappers.

Much has been said about seabirds flying to avoid the high winds of fast-moving low pressure systems (e.g. Blomqvist & Peterz 1984, Abrams 1985). However, gale-force winds of 18–21 m/s (35–40 knots) are common in the eastern boundary current regions where much of our data were collected (the same may be true for trade winds in the ETP region); winds often reach those levels in the afternoons in response to sea-land pressure differences, as the sun heats the land. With these strong winds, the seabirds present could travel hundreds of kilometers in a short period, although they may want to remain where they are, having found a particularly productive foraging "hot spot." In these conditions, most seabirds, except for the flappers and especially the heavy-body aquatic ones (and heavily molting, aquatic shearwaters), do not sit on the water. It would seem that on water they would be continually rolled by breaking waves, with danger of injury. The small species, such as storm-petrels, hide from the wind by remaining in wave troughs where wind speeds are low, as shown by their decreasing flight height in higher winds. The larger species are aloft; they likely fly so high in strong winds not only to stay out of the raging water but also to remain in the general vicinity until the winds subside to a level more manageable for feeding (or resting). In other words, they are flying but not really going anywhere, either making high loops or swoops or repeatedly returning to the same locales. Moreover, since they increase gliding and decrease flapping, they are likely expending little energy.

The heavy-body flappers (high wing-loading, e.g. loons, scoters) but also sea-anchor soarers stay low, especially with strong head- or crosswinds. This behavior is consistent with use of the wind gradient, i.e. the lower wind speeds found close to the sea surface. As wind speed increases, species exhibiting these behaviors also flap less, which is not surprising, as the wind is neutralizing their generally heavier wing loading. When flying with the wind, they fly higher, although rarely higher than 10 m. Employing more gliding and less flapping as wind speeds increase, thus decreasing flight energy, was characteristic of almost all seabirds studied.

While strong winds could blow a seabird a long way quickly, as a general rule seabirds, or at least the non-flappers, avoid flying with tailwinds (Spear & Ainley 1997a). Seemingly, seabirds have much less control in a tailwind. If they are in long-distance flight mode, they do so most efficiently with crosswinds (Pennycuick 1987a), even if using such winds takes them on a longer route (Spear & Ainley 1999a, Shaffer *et al*. 2006, Gonzales-Solis *et al*. 2009, Adams & Flora 2010). In crosswinds, the gliders, flap-gliders and glide-flappers use what is known as "gust soaring" (Pennycuick 2002), in which they use the pulses of strong winds that occur between wave crests to climb sufficiently high, without effort, to extract the wind's energy and maintain flight speed attained in the down-swoop. Pennycuick (2002) further theorized that petrels use their tubenose to sense the subtle but rapidly changing pressure gradients in order to be able to take full advantage of the narrow, between-crest wind gusts. Attaining heights of 15 m or higher in this process, at winds of 20 m/s, is not unusual. In stronger winds, the larger seabirds, and especially those with a high aspect ratio, rise even higher, perhaps looping more to minimize the horizontal distances covered, as discussed above. During migration, they take advantage of the wind energy to cover long distances quickly and somewhat effortlessly (see Shaffer *et al.* 2006: shearwaters covering approximately 1 000 km/d).

Regional differences

In our analyses, seabirds of the same flight groups tended to fly higher in either the California Current or the Antarctic compared with the ETP and Peru Current. Given that the ability to employ gust soaring is very much related to the characteristics not only of wind but of the waves as well, the difference in flight height at different locations could be related to wave height. Unfortunately, we did not collect consistent data on wave height, but, informally, we were aware of clear regional differences in wave height and behavior. The long-period swells and large waves of the Southern Ocean are legendary, and result from the unencumbered globe-circling fetch (DeBlieu 1998, Huler 2004). Without much in the way of local winds, using those swells, the larger seabirds of the Southern Ocean would be employing "slope soaring" rather than gust soaring. Slope soaring is employed by most seabirds, even those with the highest wing loading, when they ride up-currents of air along bluffs at breeding colonies; seabirds use the same principle to ride updrafts on the windward side of large ocean swells (Pennycuick 1987a). In the Antarctic (and likely the Arctic, although we have no experience there), a number of species (especially the Snow Petrel) slope-soar along the edges of ice floes (and well as icebergs), although the free-board of an ice floe is often less than a meter. Given these flight behaviors, we should expect differences in seabird flight behavior among regions with substantial differences in wave and wind conditions.

Why seabirds would fly higher in winds over the California Current than in those over the Peru Current is a more perplexing question. These two wind-current systems are completely analogous, being eastern boundary currents generated by steep pressure differentials between large offshore high pressure systems and low pressures over the adjacent land. The fetch should be about the same, as should the resulting wave regime. In both cases, we collected data during both the upwelling and the non-upwelling portions of the year. One explanation for the difference is that it could be an artifact of the locations where we sampled flight height, relative to the respective coasts. In the California Current, significant portions of cruises were close to the land (1–2 km) and especially headlands, where local wind is stronger, affecting wave conditions and gust soaring behavior. In the Peru Current, owing to the politics of national clearance, vessels were rarely closer than 20 km (12 nautical miles) from the coast, except for when entering and leaving port. Therefore, we would not have passed through the steeper local waves near the coast where gust soaring behavior would have been more prevalent.

Vulnerability of flying within the rotor-swept zone of wind generators

We defined vulnerability of flying within the rotor-swept zone as exceeding an estimated probability of 0.5 for flying at >10 m high (Table 4, Fig. 6). In general, for most flight styles, birds tended to reach this vulnerability criterion at lower wind speeds when flying into crosswinds compared with either headwinds or tailwinds. There was considerable variation in vulnerability, however, based on cluster, location, and flight direction. We considered distance offshore as a potential variable influencing vulnerability, although recent research indicates that distance offshore influences concentrations of birds, especially non-breeders, less than prey availability (e.g. Ainley *et al*. 2009).

Any of the species groups with a slope >0 in the relationship between wind and flight height (i.e. the bottom eight groups in Table 4) would be vulnerable to entering the rotor-sweep zone of most of the currently used wind turbines at the wind speeds normally prevalent in eastern boundary currents, such as the California and Peru currents or the trade winds experienced in Hawaii. These winds, typically 15–18 m/s (30–35 knots), surpass the "moderate" velocities detailed by Garthe & Hüppop (2004) and Johnston *et al*. (2013) that are used to assess seabird vulnerability for coastal Europe (see also Bradbury *et al*. 2014). It is these stronger winds that appear to have a significant effect on flight height. Those species at the top of the rank list tend to fly lower with increased wind and so would be much less vulnerable.

The relative positions of many species groups in Table 4 are consistent with the propensity of equivalent species to occur within rotor sweep zones as identified by Cook *et al*. (2012). However, there are notable exceptions, the reason for which is not clear. For example, Cook *et al*. indicate that large gulls that occur in European coastal waters are very vulnerable, where as in our analysis they are not. The reason for the difference could result from the conditions under which respective surveys were made. In our study, the large gull category is based almost entirely on sightings in the California Current of Western Gulls, and almost all of the gulls seen were commuting, often against gale-force winds, to reach their breeding colony from coastal foraging areas. During the non-breeding season, these same gulls would just sit tight on a day of strong winds, and they would not be counted in at-sea surveys. The same would be true of large alcids, deemed by Cook *et al.* (2012) not to be vulnerable. In our study, a large proportion of alcids involved were breeding Common Murres fighting very strong headwinds to return to the colony to feed chicks. The lesson here is that certain local situations need to be considered when applying our results. Presumably Cook *et al*. (2012) and others devising vulnerability indices use data amassed from widespread sources or surveys (e.g. Bradbury *et al*. 2014).

CONCLUSIONS

This study provides much-needed support for future seabird investigations of relationships between foraging ecology, behavior, morphology and wind conditions, thus increasing our understanding of natural history. In addition, this study's findings can likely contribute to the need for better information concerning potential seabird mortality of planned offshore wind energy development, although factors other than the two we studied (flight height, behavior) need to be considered (see below). Especially by location, the propensity to fly at heights >10 m (thus reaching the height of operating wind turbine rotors) and the propensity for gliding with minimal flapping were evaluated. We found that wind speed and flight direction have an important effect on flight style.

Seasonal variation in flight behavior could greatly influence where wind generators would most likely be situated. For instance, during migration in the Atlantic Flyway (not investigated herein), most waterbirds tend to use the corridor within several kilometers from shore; however, during breeding, the use of the coastal areas near breeding habitat is more predominant (Watts 2010). However, this would not apply to the Pacific Coast of North America, where seabird use, including year-round and seasonal residents and migrating species, is spread over waters covering the entire shelf and slope (Briggs *et al.* 1987, Mason *et al.* 2007). This is because bird concentration areas are associated with where prey tend to concentrate (Ainley *et al.* 2009), or biological "hot spots" (Nur *et al*. 2011), and these are not necessarily close to shore along the Pacific Coast. Seasonal ocean trends, such as differences in sea-surface temperature, wind speed and thermocline depth, which are factors that affect prey distribution, can also influence how close to shore certain species such as Sooty Shearwater, Common Murre, and Cassin's Auklet move (Oedekoven *et al*. 2001).

Avoidance behavior can considerably affect estimates of fatality risk, as several different species, particularly waterfowl (Desholm & Kahlert 2005, Fox *et al*. 2006, Masden *et al*. 2012), have been observed to avoid wind turbines. Waterfowl, however, are obligate flappers (high wing loading) and, as such, are among the least affected by winds in terms of flight height and behavior. The high speeds of swooping (flap-gliding, glide-flapping) petrels and albatross, on the other hand, with the final direction and altitude of a swoop determined by physics well in advance of its execution, probably render them incapable of avoiding structures unless they have made adjustments well in advance.

Otherwise, seabirds' responses to ocean winds have been much under-appreciated by seabird biologists, who have instead studied the more tractable aspects of direct food acquisition (e.g. depth of diving, foraging range). For example, much is known about how El Niño-Southern Oscillation (ENSO) affects food availability, but little is known about seabird shifts in response to the dramatic changes in wind and wave patterns that also occur during those events. The resulting disruption of "normal" movement patterns can be significant, and so an ENSO effect on seabirds is likely far more complex than simply an effect on food supply. As seabird biologists increasingly use telemetry and remote sensing, we may acquire new information and better appreciate seabirds' relationships to winds and waves (e.g. Suryan *et al*. 2008, Adams & Flora 2010), including interannual shifts. Pennycuick *et al.* (1984) provided initial insights into how flight behavior (and flight morphology) should be considered an important foraging niche dimension, an insight that has been appreciated rarely (e.g. Ballance 1993, Spear & Ainley 1998, Gaston 2004, Navarro *et al.* 2013). In part, this under-appreciation of at-sea bird science has been affected by biologging and instrumentation of single species, leading toward "aut-ecology" and away from community ecology.

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