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From daily movements to population distributions: weather affects competitive ability in a guild of soaring birds

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The ability of many animals to access and exploit food is dependent on the ability to move. In the case of scavenging birds, which use soaring flight to locate and exploit ephemeral resources, the cost and speed of movement vary with meteorological factors. These factors are likely to modify the nature of interspecific interactions, as well as individual movement capacity, although the former are less well understood. We used aeronautical models to examine how soaring performance varies with weather within a guild of scavenging birds and the consequences this has for access to a common resource. Birds could be divided broadly into those with low wing loading that are more competitive in conditions with weak updraughts and low winds (black vultures and caracaras), and those with high wing loading that are well adapted for soaring in strong updraughts and moderate to high winds (Andean condors). Spatial trends in meteorological factors seem to confine scavengers with high wing loading to the mountains where they out-compete other birds; a trend that is borne out in worldwide distributions of the largest species. However, model predictions and carcass observations suggest that the competitive ability of these and other birds varies with meteorological conditions in areas where distributions overlap. This challenges the view that scavenging guilds are structured by fixed patterns of dominance and suggests that competitive ability varies across spatial and temporal scales, which may ultimately be a mechanism promoting diversity among aerial scavengers.

1. Introduction

A key mechanism enabling the sympatric occurrence of animals within an ecological guild is differential access to the common resource base [1]. Thus, variation in feeding morphology [2], activity pattern (e.g. diurnal versus nocturnal [3]), ability to dominate the resource [4] and habitat use [1], all have the potential to reduce competition between species and promote coexistence. Indeed, it has been proposed that such fixed traits have led to well-structured dominance hierarchies in some systems [5,6].

Given that most animals move in order to access food resources, the efficiency of movement under any set of environmental conditions is also fundamental in defining a species competitive ability; influencing the rate at which animals can locate and arrive at a resource. Competitive ability is therefore likely to be strongly linked to habitat type as adaptations for low cost movement are often habitat specific [7,8]. Even within habitats, the costs of movement are likely to vary with conditions, such as flow strength in river systems [9], or slope angle, snow depth and grass height for terrestrial animals [10,11]. Consequently, in heterogeneous environments, competitive ability is likely to vary in space and time according to trends in movement costs [1].

The costs of, and capacities for, movement are particularly pertinent for animals that exploit ephemeral food resources, including carrion [12]. For example, both avian and mammalian scavengers target sparsely distributed carrion, yet model studies have shown that soaring birds will always outcompete their

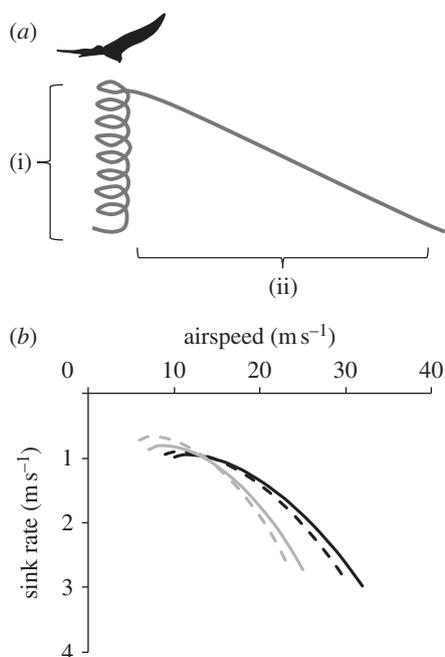


Figure 1. (a) Cross-country flight typically involves (i) a soaring phase where the bird gains altitude in an updraught and (ii) a gliding phase. Birds are predicted to fly at speeds that minimize their rate of sink (V_{ms}) while soaring, and maximize their horizontal range per unit altitude (V_{bg}) during the glide. (b) These speeds can be predicted from the glide polar for any given individual, with V_{ms} being the airspeed with the lowest sink rate, and V_{bg} derived by taking the tangent to the polar curve. Glide polars are given for four scavengers (male condor given as a solid black line, female condor a dashed black line, black vulture a solid grey line, caracara a dashed grey line).

terrestrial mammalian counterparts because of their low cost of transport (COT) and the ability to arrive at a food patch quickly [13]. Within avian scavengers, birds using soaring flight outcompete those that use flapping flight due to the reduction in transport costs, despite the latter being faster [13]. Consequently, the capacity for soaring flight is fundamental to the competitive ability of avian scavengers, making them a good model system with which to examine how environmental variation affects competitive ability. However, to date, environmentally invariant features, such as morphological adaptations for feeding have received much greater attention, with a range of studies showing that Old World vultures can be grouped into three consistent categories according to their skull dimensions and beak strength, which are associated with the parts and size of a carcass they target [2,5,14].

Soaring birds achieve a low COT by gaining altitude in updraughts (environmentally generated sources of rising air), and gliding to another location, thereby reducing or obviating the need for flapping flight [15,16]. Several key aspects of gliding performance, including the cross-country speed (the overall groundspeed achievable in cycles of soaring and gliding; figure 1a), are fundamentally and predictably related to morphology and can be estimated using the principles of aeronautical engineering [17–19], where morphological parameters are known. Indeed, Pennycuick [20] used this approach to show that wing loading (a bird's body weight as a function of its wing area) is negatively correlated with the strength and diameter of updraughts a bird can use to remain airborne. Updraughts used by birds can be broadly categorized as 'thermals', which are generated by heating effects, and orographic/slope lift, which occurs where wind is deflected upwards by

sloping terrain. While cross-country speed has been estimated in relation to thermal characteristics for a range of species [15,20], variation in performance in relation to wind-generated updraughts has yet to be explored. This may be because many soaring birds are known to fly along slopes during their migrations [21], which may have led to the assumption that birds undertaking daily foraging movements use slopes in the same manner. Nonetheless, recent evidence suggests that birds use altitude gained over slopes to travel both along and away from these features in search of food (S. Lambertucci *et al.* 2010–2013, unpublished data). Furthermore, it is important to explore the consequences of movement in a range of wind speeds, as birds must fly faster than the wind in order to move in a direction that is independent from it [22], and flight speed is linked fundamentally to gliding range.

The aim of this study was to predict how competitive ability varies within a group of sympatric scavenging birds under a range of meteorological scenarios (using aeronautical models), and examine whether these predictions are supported by observations of scavenger abundance at experimentally placed carcasses. Our hypotheses were (i) that cross-country speed varies according to weather variables and wing loading and (ii) that these environmentally mediated changes in performance are, in turn, linked to encounter rate. The expectation is that larger birds (with high wing loading) achieve higher cross-country speeds when strong updraughts are available, thus providing them with a competitive advantage under these conditions. The study was undertaken in northwest Patagonia, where crested caracaras (*Polyborus plancus*), black vultures (*Coragyps atratus*) and Andean condors (*Vultur gryphus*) commonly aggregate at the same carcass, representing perhaps the world's largest range in body mass for sympatric soaring scavengers (*ca* 1.3–15 kg), although other systems have analogous scavenger assemblages [2,23]. While dominance at the carcass is usually correlated with body mass [6], with the Andean condor outcompeting all other species, black vultures are able to monopolize the carcass when they occur in sufficient numbers [24]. Consequently, the competitive ability of condors and black vultures is affected by the speed at which they can access the carcass. While a range of studies have examined the abundance and arrival times of scavengers at carrion in general [2,25,26], the role of meteorological variables has yet to be investigated systematically.

2. Material and methods

Wing measurements were taken from birds captured with baited cannon net traps in northwest Argentine Patagonia [16], with all birds being kept in the shade during the process. Wing drawings were made for six male and six female Andean condors, 16 black vultures and four crested caracaras, following Pennycuick [27]. Separate measurements were obtained for male and female condors as males are 30–40% heavier than females [23], which is likely to have a profound impact on their soaring performance. Bird body mass was also measured and loggers were fitted to some individuals [16] before birds were released.

The freeware 'Flight 1.24' [27] (<http://books.elsevier.com/companions/9780123742995>) was used to estimate glide polars for the different species, using wing measurements from a single representative individual, which was selected on the basis of having an average body mass and wing span for the birds captured. The glide polar gives the estimated sink rate of the bird for any flight speed [27], and can therefore be used to derive the airspeed associated with the minimum sink rate

(V_{ms}), and the maximum distance travelled per metre of altitude lost, i.e. the 'best glide' speed (V_{bg}) [27]. These parameters were used to produce simplistic models to estimate how gliding performance varied for the different species when relying on (i) thermal updraughts and (ii) orographic lift (see below).

The cross-country speed was taken as a measure of the movement capacity of any individual as a function of the environmental conditions for a given model scenario (although we note that other factors, such as search pattern will affect overall encounter rates). The cross-country speed refers to the groundspeed achieved by a bird that climbed in an updraught (with no net change in position) and converted this altitude into horizontal distance by gliding (figure 1a). This speed is likely to be related to the competitive ability of a species, as faster groundspeeds should lead to higher food encounter rates. The COT would provide another putative measure of competitive ability; however, this would be unlikely to add substantially to the model, being inversely related to cross-country speed. Furthermore, the estimation of COT would require additional assumptions about soaring metabolic rate. The current approach assumes that model birds do not vary in their ability to access updraughts and that all species are equally likely to detect carrion.

(a) Performance in thermals

Flight performance was examined by calculating several parameters in relation to model thermal updraughts (hereafter 'thermals') that varied in strength from 1 to 5 m s⁻¹, representing a range of weak to strong updraughts [15]. The cross-country speed is a function of the rate of climb in a thermal (the thermal strength less the minimum sink rate of the bird) and the inter-thermal glide speed, which was taken as V_{bg} [17,28]. The duration of the glide phase is simply the altitude gained divided by the sink rate when the bird is flying at V_{bg} , and the groundspeed is the duration of the flight divided by the horizontal distance flown. Hence the groundspeed is independent of the distance covered as this will be the same whether the bird climbed 1 or 100 m in a thermal. The model assumes therefore, that the bird is able to gain sufficient altitude to glide to its destination, either by encountering frequent thermals or gaining enough altitude in one thermal, but without employing flapping flight.

The cross-country speed, costs of flight and range will all be affected by the choice of speed during the glide phase. V_{bg} is defined as the speed with the highest glide ratio, i.e. the highest glide distance per unit altitude gained. V_{bg} was selected as one possible strategy, with another being the selection of the 'MacCready speed' [27], which increases with the strength of updraughts encountered and maximizes the cross-country speed. As it is not the absolute speeds that are of particular interest, but the broad relationships between species, the selection of one or the other speed is less critical. Furthermore, if birds increased their glide speed, this would increase the relative importance of the glide ratio, which would only serve to exaggerate the differences between species. The main assumption made in the model is therefore that all species use the same strategy.

(b) Performance in orographic lift

In this scenario, model birds gained altitude by soaring in orographic lift and then used this altitude to glide away from the lift. The strength of lift was derived as a function of a range of wind speeds and slope angles using trigonometry, assuming, for simplicity, that wind blows directly and uniformly up the slope. The soaring phase here is analogous to that in the thermal scenario, with the climb rate being the difference between the bird's minimum sink rate and the strength of the lift. The groundspeed during the glide phase is altered by the inclusion of wind, such that, once a bird begins to glide it moves either into the wind or with it (i.e. head- and tail-wind scenarios).

This is particularly ecologically relevant in regions with persistent winds, such as Patagonia, where birds cannot return to a central place without flying against headwind.

In the study region, the monthly mean wind speed is 5.1–8.2 m s⁻¹ with hourly means typically ranging from 0 to 14 m s⁻¹ from November to February (as recorded at Bariloche airport, 41.1520° S, 71.1584° W). Groundspeed was estimated for model birds flying in a conservative range of winds, from a light breeze to a moderate wind. Groundspeed was calculated assuming that there was no net change in location while the bird was gaining altitude, but that when the bird left the source of lift it flew at V_{bg} for the wind encountered. This was estimated by calculating the glide ratio (using groundspeed) for all bird–wind combinations. This value of V_{bg} and associated sink rate were then used to estimate the duration of a glide, and hence the overall time taken, for a given climb–glide cycle. Therefore, the main assumption is that birds increase their airspeed in a headwind and reduce it in a tailwind, as predicted by optimal migration theory ([29–31], see also [32]).

(c) Scavenger abundance and meteorological conditions

Twelve carcasses were placed within a single farm where all three scavenger species fed during the Austral summers of 2008 (six), 2010 (two) and 2011 (four). The maximum number of scavengers at the carcass was determined between 08.00 and 10.00 and between 14.00 and 16.00, chosen probably to represent weak and strong thermal scenarios, respectively [15]. Two proxies were used for the availability and strength of updraughts in the mid-points of these observational periods (09.00 and 15.00) (i) mean hourly wind speed, which was available for the meteorological station at Bariloche airport, 4.3–11.7 km from the observation sites and (ii) the convective velocity scale, w^* , which is proportional to the mean thermal strength [21]

$$w^* = \left[\frac{gzH}{T} \right]^{1/3}, \quad (2.1)$$

where g is the gravitational acceleration, z the height of the planetary boundary layer, H the surface heat flux and T the potential temperature in Kelvin. Values of w^* were calculated for the geographical coordinates closest to the study area (ca 30 km to the northeast), where predicted values of z and H were obtained from NASA reanalysis data (specifically from MERRA), which are model-observation hybrid data [33]. Values of T were calculated using temperature and pressure outputs from MERRA, following Bohrer *et al.* [21].

Generalized linear models (GLMs) were used to assess whether scavenger abundance (error distribution: Poisson, link function: logarithmic, dependent variable: number of Andean condors, black vultures or crested caracaras per 2 h period) was predicted by wind velocity, w^* , and the abundance of the other species (AC, BV, CC) also present at the carcass. Year and carcass were also included in the models, and over-dispersion was controlled for when necessary. Effects were considered significant when $p \leq 0.05$.

3. Results

Species could be grouped into two broad categories based on their glide polars, with the performance of the male and female condors being substantially different from those of the caracara and black vulture (figure 1b). The condors had higher minimum sink rates but faster flight speeds for a given sink rate (for those sink rates predicted for both groups, i.e. from ca 1.2 m s⁻¹). Consequently, condors should be well adapted for fast flight where there is strong environmental lift, as well as flight during stronger winds.

Table 1. Morphological parameters for each of the birds for which the glide polar was estimated, with predicted values of true airspeed and sink rates at the minimum sink (V_{ms}) and best glide (V_{bg}) speeds.

		body mass (kg)	wing area (m ²)	wing loading (N m ⁻²)	V_{ms}		V_{bg}	
					speed (m s ⁻¹)	sink rate (m s ⁻¹)	speed (m s ⁻¹)	glide ratio
Andean condor	male	13.30	1.06	123.09	11.4	1.0	17.8	15.1
Andean condor	female	10.70	1.02	102.91	10.5	0.9	16.5	14.7
black vulture	—	2.05	0.31	65.08	8.6	0.8	13.6	13.5
crested caracara	—	1.30	0.26	48.49	7.4	0.7	11.7	14.0

The black vulture and caracara should be better adapted to low-lift scenarios due to their low minimum sink rates, which enable them to exploit weaker updraughts.

(a) Performance in thermals

The strength of the updraught must exceed the minimum sink rate (V_{ms}) for birds to gain altitude within them. Estimates of V_{ms} were 0.67, 0.81, 0.90 and 0.95 m s⁻¹ for the caracara, black vulture, female and male condor, respectively (table 1). When thermal velocity was low relative to the bird sink rate, the cross-country speed was negatively correlated with wing loading. This relationship reversed as the rate of climb increased beyond approximately 1.5 m s⁻¹, where the proportion of the journey spent gliding between sources of lift increased. As thermals increased in strength above 1.5 m s⁻¹, so too did the difference between the groundspeeds of the condor and the other birds (figure 2).

(b) Performance in orographic lift

Groundspeed was predicted to increase with slope angle and wind strength for all birds, although the increase was greater for condors. The only circumstance under which black vultures and caracaras were predicted to achieve higher groundspeeds was with light winds, where these birds could achieve faster speeds using slopes of up to 40° (figure 3). This was similar whether birds were operating with a headwind or tailwind.

The range of slope angles that birds could use to remain airborne increased with wind speed (figure 4a), with the minimum usable slope angle varying from a mean of 25° with a 2 m s⁻¹ wind, to 6° with an 8 m s⁻¹ wind. The glide ratio decreased as the headwind increased for all species, although the gap between the condors and the caracara and black vulture increased with wind speeds over *ca* 2 m s⁻¹ (figure 4b). The glide ratio increased with a tailwind for all species, but interspecific differences were not clearly related to wing loading (figure 4c).

(c) Scavenger abundance at carcasses

Observations of scavenger abundance were made over 51 days and a wide range of meteorological conditions, excluding persistent precipitation, with mean hourly wind speed ranging from 0 to 14 m s⁻¹ per observation period. The maximum number of birds in a 2 h period was 54 condors, 73 black vultures and 25 caracaras. The abundance of Andean condors was positively influenced by wind speed (Wald = 9.23, $p = 0.002$), whereas black vulture numbers were positively

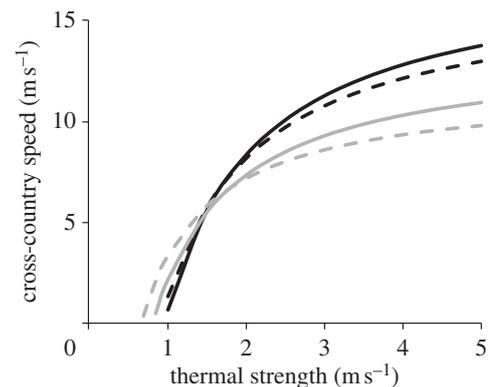


Figure 2. The predicted cross-country speed according to thermal strength for four scavengers (male condor is shown by a solid black line, female condor a dashed black line, black vulture a solid grey line, and caracara a dashed grey line).

related to the abundance of crested caracaras (Wald = 24.44; $p < 0.001$), and the presence of caracaras was negatively related to w^* (Wald = 11.04, $p < 0.001$) and positively to the abundance of black vultures (Wald = 80.94; $p < 0.001$).

4. Discussion

The prevailing conditions will always affect species differentially, irrespective of what the conditions are. In our study system, where birds share a similar wing shape, the differences in movement capacity are largely due to patterns of body size. For instance, while aeronautical models predict that all birds experience an increase in movement efficiency associated with an increase in the strength of environmental lift (a trend likely to apply to all flying birds [34]), larger birds, which typically have higher wing loading [27] (table 1), are predicted to profit to a greater extent (figure 2). Larger birds are also predicted to suffer less of a reduction in gliding efficiency with increasing headwind strength. While our field results are preliminary, they provide some support for the hypothesis that weather-related differences in performance affect access to food resources (cf. [1]). To date there have been few such demonstrations, though the effects of the environment on the movement costs of individual species are widely documented [15,34–36]. The abundance of condors was related to wind speed.

The abundance of condors was related to wind speed (as predicted), although the abundance of black vultures and caracaras was not. These smaller species are likely to be more sensitive to increases in wind speed (figure 4), and it may be

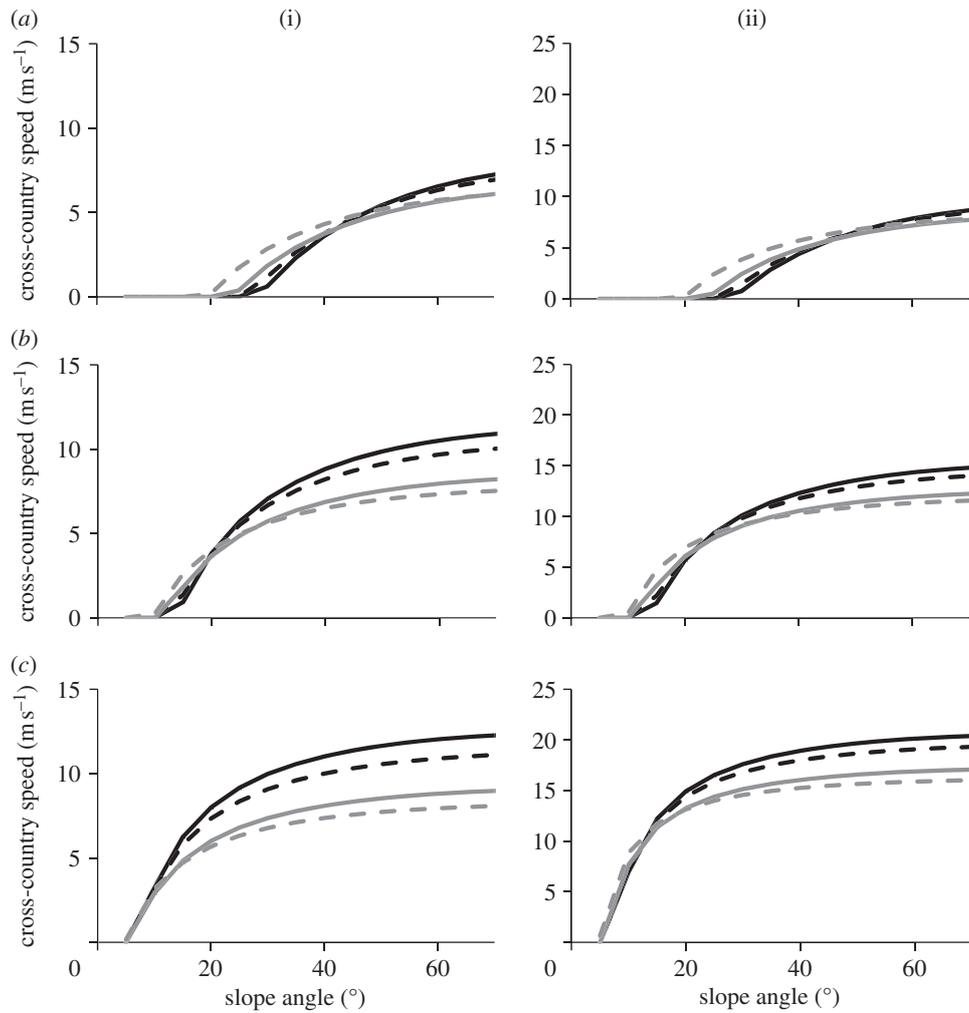


Figure 3. The predicted cross-country speed for four scavengers (male condor given as a solid black line, female condor a dashed black line, black vulture a solid grey line, and caracara a dashed grey line) soaring in orographic lift with wind strengths of (a) 2 m s^{-1} (b) 4 m s^{-1} and (c) 8 m s^{-1} , where a–c(i) indicate a headwind and a–c(ii) indicate a tailwind.

that they refuge from higher wind speeds by selecting lower flight heights. Nonetheless, caracaras do appear to select lower lift scenarios, where models predict that they have a competitive advantage, as their numbers decreased with increasing thermal strength (w^*). The numbers of black vultures and caracaras were positively correlated, which is consistent with their similarities in their soaring performance. However, these birds are considered potential competitors [6] and their co-occurrence here may also be facilitated by the large carrion used in this study. That condor abundance was not related to thermal strength is in contrast to the findings of Wallace & Temple [6], who documented that condors were usually the last of five species of scavenger to arrive, suggesting condors may be less competitive early in the morning. Our results may therefore reflect the coarser temporal resolution of observations at the carcass (and associated measures of w^*) in relation to the rate of thermal development and the condor's predicted sensitivity to it.

Competitive ability is typically considered in relation to relatively static conditions, that is, environments that change over seasonal scales or display reasonably constant spatial heterogeneity [1,3,37]. Nonetheless, interspecific interactions may be modulated where change does occur: for instance, snow depth alters the outcome of interactions between grey wolves (*Canis lupus*) and elk (*Cervus canadensis*) according to the body size of the elk and ability to move through increasing snow depth [38]. In stark contrast to terrestrial systems, fluid

media are highly dynamic, and changes with greater consequences for movement efficiency occur over much shorter timescales [39]. For instance, thermal convection is frequently shut-down by cloud cover, which may force soaring birds to switch to flapping flight. Equally, an increase in wind strength will reduce the glide ratio of birds heading into wind and may ultimately result in birds no longer being able to make headway. Such changes occur over scales of hours to seasons and the implications for flying avifauna are profound.

Meteorological conditions also vary spatially, and therefore we might expect geographical patterns in competitive ability. Mountains are 'high-lift' habitat, as thermals are generated by the rapid heating of mountain slopes, as well as the increased solar radiation, cooler climates and lower atmospheric moisture typical of higher elevations [40]. Furthermore, when wind strength increases, so does the availability of slope lift [41]. By contrast, thermals in flat regions become increasingly flattened and then disrupted as the wind speed approaches and exceeds the vertical component of the thermal vector. Thus, mountain habitat is associated with strong updraughts year-round, while flat-lands generate only strong updraughts in periods of low wind strength [40]. Given the extensive search times associated with scavenging [13], and the strong lift required by larger birds to soar, it is perhaps unsurprising that large vultures are distributed in areas of topographic relief [23,42]. In fact, within the 23 vulture species, body size is generally correlated with the degree of relief with all four

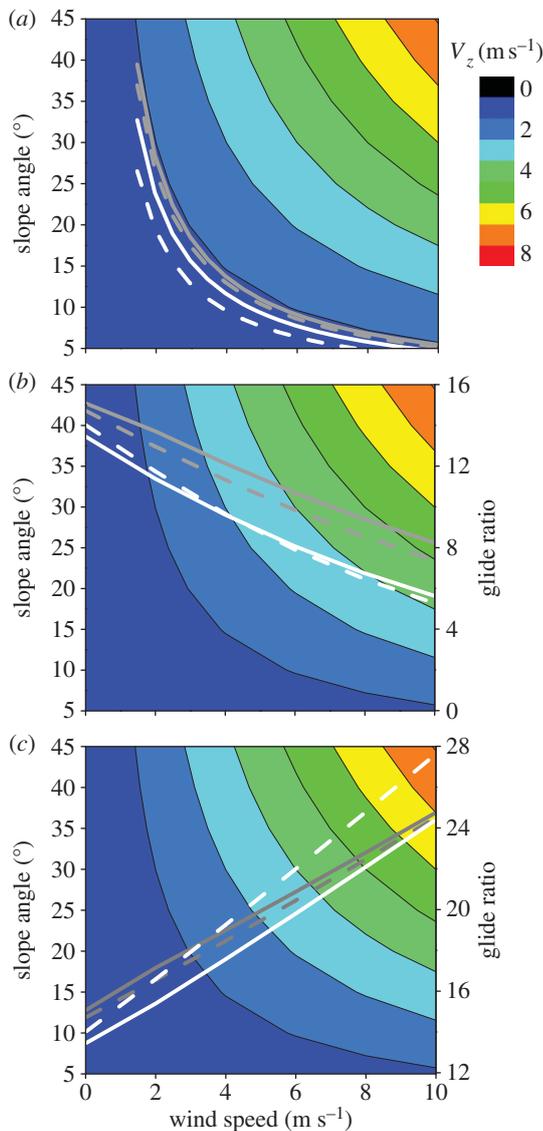


Figure 4. The strength of orographic lift (V_z) produced by different combinations of wind speed and slope angle is shown in colour, where wind blows directly up a slope. (a) Superimposed upon this are contours indicating the minimum slope lift required for each of four scavengers to remain aloft (male condor shown as a solid grey line, female condor a dashed grey line, black vulture a solid white line and caracara a dashed white line). Birds can remain aloft for any wind speed/slope angle combination to the right and above any of the lines. (b) Higher wind speeds will generate higher rates of climb for any given slope angle, however, birds flying into stronger headwinds will experience a reduction in glide ratio (given as solid and dashed lines for individuals gliding into wind). Consequently, birds may not select their flight route on the basis of climb rate alone. Glide ratios for birds flying with tailwinds are given as solid and dashed lines in (c).

species with a mean body mass more than 9 kg (as well as the bearded vulture (*Gypaetus barbatus*) 4.5–7.5 kg) being confined to the highest and most extensive mountain ranges [23]. In certain cases, this holds within species as the body mass of Cinereous vultures (*Aegypius monachus*) in southwest Europe is

on average 10% less than those in Asia, which occur in more mountainous habitat [43].

Overall therefore, this suggests that spatial patterns in meteorological variables affect regional-scale distributions of scavengers, confining birds with a high body mass to mountainous regions where they generally out-compete smaller scavengers in terms of their ability to exploit large carcasses [4,6]. In the present study area, the abrupt transition from mountain to relatively flat steppe habitat east of the Andes, marks a shift from strong to weak updraughts (due to the high winds speeds characteristic of the region [44]), and a concomitant reduction in the movement capacity of condors, which require environmental lift to remain airborne [45]. Yet, as wind or thermal strength increases, so too does the ability of condors to exploit lower slope angles and move into the steppe. This is likely to produce spatial patterns in movement capacity and competitive ability that vary with meteorological conditions.

Environmentally driven variation in competitive advantage can therefore occur from diurnal to seasonal and climatological scales (cf. [2,14]), and it could be that, over time, this promotes diversity among aerial scavengers [46]. Although it is worth noting that scavengers may not experience a pure form of competitive exclusion, as in other systems, for example, the presence of one species at a carcass may facilitate access for another by indicating the location of a carcass or by physically opening it ([2], cf. [24]). Further investigation into the scavengers that predominate at carcasses for a given set of weather and landscape variables [47], as well as the nature of interspecific interactions within other guilds of volant animals, such as marine scavengers [48] and insectivores, could provide insight into the role of movement costs and performance in modulating interspecific competition in a general sense. In the case of soaring scavengers, this may provide insights into the conditions under which animals are likely to struggle or thrive, which may be particularly pertinent given the conservation status of many vultures [49].

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References

1. Brown JS. 1989 Desert rodent community structure: a test of four mechanisms of coexistence. *Ecol. Monogr.* **59**, 1–20. (doi:10.2307/2937289)
2. Kruuk H. 1967 Competition for food between vultures in East Africa. *Ardea* **55**, 171–193.
3. Wauters LA, Gurnell J, Martinoli A, Tosi G. 2002 Interspecific competition between native Eurasian red squirrels and alien grey squirrels: does resource

- partitioning occur? *Behav. Ecol. Sociobiol.* **52**, 332–341. (doi:10.1007/s00265-002-0516-9)
4. Donazar JA, Travaini A, Ceballos O, Rodriguez A, Delibes M, Hiraldo F. 1999 Effects of sex-associated competitive asymmetries on foraging group structure and despotic distribution in Andean condors. *Behav. Ecol. Sociobiol.* **45**, 55–65. (doi:10.1007/s002650050539)
 5. Hertel F. 1994 Diversity in body size and feeding morphology within past and present vulture assemblages. *Ecology* **75**, 1074–1084. (doi:10.2307/1939431)
 6. Wallace MP, Temple SA. 1987 Competitive interactions within and between species in a guild of avian scavengers. *Auk* **104**, 290–295.
 7. Dickinson MH, Farley CT, Koehl MAR, Kram R, Lehman S. 2000 How animals move: an integrative view. *Science* **288**, 100–106. (doi:10.1126/science.288.5463.100)
 8. Wilson RP. 2010 Resource partitioning and niche hyper-volume overlap in free-living Pygoscelid penguins. *Funct. Ecol.* **24**, 646–657. (doi:10.1111/j.1365-2435.2009.01654.x)
 9. McElroy B, DeLonay A, Jacobson RB. 2012 Optimum swimming pathways of fish spawning migrations in rivers. *Ecology* **93**, 29–34. (doi:10.1890/11-1082.1)
 10. Fancy SG, White RG. 1987 Energy expenditures for locomotion by barren-ground caribou. *Can. J. Zool.* **65**, 122–128. (doi:10.1139/z87-018)
 11. Wall J, Douglas-Hamilton I, Vollrath F. 2006 Elephants avoid costly mountaineering. *Curr. Biol.* **16**, 527–529. (doi:10.1016/j.cub.2006.06.049)
 12. Carbone C, Turvey ST, Bielby J. 2011 Intra-guild competition and its implications for one of the biggest terrestrial predators, *Tyrannosaurus rex*. *Proc. R. Soc. B* **278**, 2682–2690. (doi:10.1098/rspb.2010.2497)
 13. Ruxton GD, Houston DC. 2004 Obligate vertebrate scavengers must be large soaring fliers. *J. Theor. Biol.* **228**, 431–436. (doi:10.1016/j.jtbi.2004.02.005)
 14. Houston DC. 1975 Ecological isolation of African scavenging birds. *Ardea* **63**, 55–64.
 15. Pennycuik CJ. 1972 Soaring behavior and performance of some East African birds, observed from a motor-glider. *Ibis* **114**, 178–218. (doi:10.1111/j.1474-919X.1972.tb02603.x)
 16. Shepard ELC, Lambertucci SA, Vallmitjana D, Wilson RP. 2011 Energy beyond food: foraging theory informs time spent in thermals by a large soaring bird. *PLoS ONE* **6**, e27375. (doi:10.1371/journal.pone.0027375)
 17. Akos Z, Nagy M, Vicssek T. 2008 Comparing bird and human soaring strategies. *Proc. Natl Acad. Sci. USA* **105**, 4139–4143. (doi:10.1073/pnas.0707711105)
 18. Chatterjee S, Templin RJ, Campbell KE. 2007 The aerodynamics of *Argentavis*, the world's largest flying bird from the Miocene of Argentina. *Proc. Natl Acad. Sci. USA* **104**, 12 398–12 403. (doi:10.1073/pnas.0702040104)
 19. Pennycuik CJ. 1997 Actual and 'optimum' flight speeds: field data reassessed. *J. Exp. Biol.* **200**, 2355–2361.
 20. Pennycuik CJ. 1971 Gliding flight of white-backed vulture *Gyps africanus*. *J. Exp. Biol.* **55**, 13–38.
 21. Bohrer G, Brandes D, Mandel JT, Bildstein KL, Miller TA, Lanzone M, Katzner T, Maisonneuve C, Tremblay JA. 2011 Estimating updraft velocity components over large spatial scales: contrasting migration strategies of golden eagles and turkey vultures. *Ecol. Lett.* **15**, 96–103. (doi:10.1111/j.1461-0248.2011.01713.x)
 22. Chapman JW, Klaassen RHG, Drake VA, Fossette S, Hays GC, Metcalfe JD, Reynolds AM, Reynolds DR, Alerstam T. 2011 Animal orientation strategies for movement in flows. *Curr. Biol.* **21**, 861–870. (doi:10.1016/j.cub.2011.08.014)
 23. Del Hoyo J. 1994 *Handbook of the birds of the world*, vol. 2. Barcelona, Spain: Lynx.
 24. Carrete M, Lambertucci S, Speziale K, Ceballos O, Travaini A, Delibes M, Hiraldo F, Donazar JA. 2010 Winners and losers in human-made habitats: interspecific competition outcomes in two neotropical vultures. *Anim. Conserv.* **13**, 390–398. (doi:10.1111/j.1469-1795.2010.00352.x)
 25. Houston DC. 1974 Food searching in griffon vultures. *Afr. J. Ecol.* **12**, 63–77. (doi:10.1111/j.1365-2028.1974.tb00107.x)
 26. Lambertucci SA, Speziale KL, Rogers TE, Morales JM. 2009 How do roads affect the habitat use of an assemblage of scavenging raptors? *Biodiv. Conserv.* **18**, 2063–2074. (doi:10.1007/s10531-008-9573-3)
 27. Pennycuik CJ. 2008 *Modelling the flying bird*. London, UK: Elsevier.
 28. Spaar R, Bruderer B. 1997 Optimal flight behavior of soaring migrants: a case study of migrating steppe buzzards, *Buteo buteo vulpinus*. *Behav. Ecol.* **8**, 288–297. (doi:10.1093/beheco/8.3.288)
 29. Liechti F. 1995 Modelling optimal heading and airspeed of migrating birds in relation to energy expenditure and wind influence. *J. Avian Biol.* **26**, 330–336. (doi:10.2307/3677049)
 30. Pennycuik CJ. 1978 15 Testable predictions about bird flight. *Oikos* **30**, 165–176. (doi:10.2307/3543476)
 31. Alerstam T, Gudmundsson GA, Larsson B. 1993 Flight tracks and speeds of Antarctic and Atlantic seabirds: radar and optical measurements. *Phil. Trans. R. Soc. Lond. B* **340**, 55–67. (doi:10.1098/rstb.1993.0048)
 32. Shamoun-Baranes J, van Loon E, Liechti F, Bouten W. 2007 Analyzing the effect of wind on flight: pitfalls and solutions. *J. Exp. Biol.* **210**, 82–90. (doi:10.1242/jeb.02612)
 33. Rienecker MM *et al.* 2011 MERRA: NASA's modern-era retrospective analysis for research and applications. *J. Climate* **24**, 3624–3648. (doi:10.1175/JCLI-D-11-00015.1)
 34. Sapir N, Wikelski M, McCue MD, Pinshow B, Nathan R. 2010 Flight modes in migrating European bee-eaters: heart rate may indicate low metabolic rate during soaring and gliding. *PLoS ONE* **5**, e13956. (doi:10.1371/journal.pone.0013956)
 35. De Monte S, Cotté C, d'Ovidio F, Lévy M, Le Corre M, Weimerskirch H. 2012 Frigatebird behaviour at the ocean–atmosphere interface: integrating animal behaviour with multi-satellite data. *J. R. Soc. Interface* **9**, 3351–3358. (doi:10.1098/rsif.2012.0509)
 36. Weimerskirch H, Louzao M, De Grissac S, Delord K. 2012 Changes in wind pattern alter albatross distribution and life-history traits. *Science* **335**, 211–214. (doi:10.1126/science.1210270)
 37. Connell JH. 1983 On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* **122**, 661–696. (doi:10.1086/284165)
 38. Huggard DJ. 1993 Effect of snow depth on predation and scavenging by gray wolves. *J. Wildl. Manage* **57**, 382–388. (doi:10.2307/3809437)
 39. Shepard ELC, Wilson RP, Rees WG, Grundy E, Lambertucci SA, Vosper SB. 2013 Energy landscapes shape animal movement ecology. *Am. Nat.* **182**, 298–312. (doi:10.1086/671257)
 40. Bradbury T. 2004 *Meteorology and flight: a pilot's guide to weather*. London, UK: A&C Black Publishers Ltd.
 41. Vosper S. 2003 Development and testing of a high resolution mountain-wave forecasting system. *Meteorol. Appl.* **10**, 75–86. (doi:10.1017/S1350482703005085)
 42. Houston DC. 1983 The adaptive radiation of the griffon vultures. In *Vulture biology and management* (eds SR Wilbur, JA Jackson), pp. 135–152. Berkeley, CA: University of California Press.
 43. Ferguson-Lees J, Christie DA. 2001 *Raptors of the world*. London, UK: Christopher Helm.
 44. Paruelo JM, Beltran A, Jobbagy E, Sala OE, Golluscio RA. 1998 The climate of Patagonia: general patterns and controls on biotic. *Ecol. Austral* **8**, 85–101.
 45. McGahan J. 1973 Flapping flight of the Andean condor in nature. *J. Exp. Biol.* **58**, 239–253.
 46. Jetz W, Rahbek C. 2002 Geographic range size and determinants of avian species richness. *Science* **297**, 1548–1551. (doi:10.1126/science.1072779)
 47. Cortés-Avizanda A, Carrete M, Donazar JA. 2010 Managing supplementary feeding for avian scavengers: guidelines for optimal design using ecological criteria. *Biol. Conserv.* **143**, 1707–1715. (doi:10.1016/j.biocon.2010.04.016)
 48. Phillips RA, Silk JRD, Croxall JP. 2005 Foraging and provisioning strategies of the light-mantled sooty albatross at South Georgia: competition and co-existence with sympatric pelagic predators. *Mar. Ecol. Prog. Ser.* **285**, 259–270. (doi:10.3354/meps285259)
 49. Pain DJ *et al.* 2003 Causes and effects of temporospatial declines of *Gyps* vultures in Asia. *Conserv. Biol.* **17**, 661–671. (doi:10.1046/j.1523-1739.2003.01740.x)