




# Physical limits of flight performance in the heaviest soaring bird

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**Flight costs are predicted to vary with environmental conditions, and this should ultimately determine the movement capacity and distributions of large soaring birds. Despite this, little is known about how flight effort varies with environmental parameters. We deployed bio-logging devices on the world's heaviest soaring bird, the Andean condor (*Vultur gryphus*), to assess the extent to which these birds can operate without resorting to powered flight. Our records of individual wingbeats in >216 h of flight show that condors can sustain soaring across a wide range of wind and thermal conditions, flapping for only 1% of their flight time. This is among the very lowest estimated movement costs in vertebrates. One bird even flew for >5 h without flapping, covering ~172 km. Overall, > 75% of flapping flight was associated with takeoffs. Movement between weak thermal updrafts at the start of the day also imposed a metabolic cost, with birds flapping toward the end of glides to reach ephemeral thermal updrafts. Nonetheless, the investment required was still remarkably low, and even in winter conditions with weak thermals, condors are only predicted to flap for ~2 s per kilometer. Therefore, the overall flight effort in the largest soaring birds appears to be constrained by the requirements for takeoff.**

aerocology | energy landscape | biologging | flight constraints | movement ecology

Gradients in energy have been invoked to explain macroecological patterns including species distribution and abundance (1, 2). While the main forms of available energy are typically identified as photosynthetically active radiation and chemical energy (reviewed in ref. 3), flying animals extract kinetic and potential energy from the environment by soaring, and use this energy to subsidize the metabolic costs of flapping flight. Therefore, flight costs and capacities in animals are fundamentally linked to the characteristics of air currents (4–6), and this affects large-scale patterns of space use. For instance, passerine birds tune their migration decisions in relation to the wind (7) and use particular migration flyways that are not necessarily associated with the shortest route (8–10). Outside of migration, it is the ecology of soaring flight specialists that should be most closely linked to environmental conditions (11–14). Indeed, for the very largest flying birds, the dependence on soaring is such that their distributions appear to be linked to, and potentially constrained by, the availability of updrafts or wind shear (5).

Soaring specialists tend to be large birds (but see refs. 15 and 16), as the selective pressure to extract energy from the aerial environment is related to the costs of powered flight, which increase more or less proportionately with body size ( $Mass^{1.17}$ ) (17). In contrast, the costs of soaring appear to be approximately twice the resting requirement (18–20), which itself decreases with increasing mass (being proportional to  $Mass^{0.67}$ ) (21). Therefore, the disparity between the metabolic costs of soaring and flapping increases with animal mass, so that for large birds, the cost of flapping flight is predicted to be some 30 times greater than resting metabolic costs (22). This puts flapping flight in the same bracket as other high-performance activities, such as sprinting in mammals (23), which individuals should undertake only when

absolutely necessary. Large soaring birds are most likely to flap to remain airborne or increase speed at times when they are unable to soar. Knowing the extent to which aerial conditions force large birds to use powered flight is key to understanding how their movements and space-use are constrained by the physical environment (12).

Examining when and where obligate soarers resort to flapping should also provide insight into the particular conditions that might have supported the flight of the largest birds ever to have flown (24). The largest extant soaring birds weigh up to almost 16 kg (25), but extinct terrestrial birds were much larger, with the largest, *Argentavis magnificens*, estimated to have weighed ~72 kg or more (24). It has always been assumed that *Argentavis* would have been incapable of sustained flapping flight and thus entirely dependent on soaring. Nonetheless, almost nothing is known about the amount of flapping flight required for daily foraging movements even in large extant soaring birds (26–28).

In the present study, we assessed whether, and if so, how, flight effort varies with environmental conditions in the world's heaviest extant soaring bird, the Andean condor (*Vultur gryphus*). Given that flapping was likely to be relatively infrequent, we developed custom logging and tag-release systems to obtain uninterrupted, high-frequency data on the flight behavior of these birds. These

## Significance

**Flapping flight is extremely costly for large birds, yet little is known about the conditions that force them to flap. We attached custom-made “flight recorders” to Andean condors, the world's heaviest soaring birds, documenting every single wingbeat and when and how individuals gained altitude. Remarkably, condors flapped for only 1% of their flight time, specifically during takeoff and when close to the ground. This is particularly striking as the birds were immature. Thus, our results demonstrate that even inexperienced birds can cover vast distances over land without flapping. Overall, this can help explain how extinct birds with twice the wingspan of condors could have flown.**

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The authors declare no competing interest.

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Data deposition: GPS and Daily Diary data for the eight condors have been uploaded to the Movebank database under the study “Andean Condor (*Vultur gryphus*), Bariloche, Argentina, 2013–2018” ([https://www.movebank.org/cms/webapp?gwt\\_fragment=page=studies,path=study1109284853](https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1109284853)).

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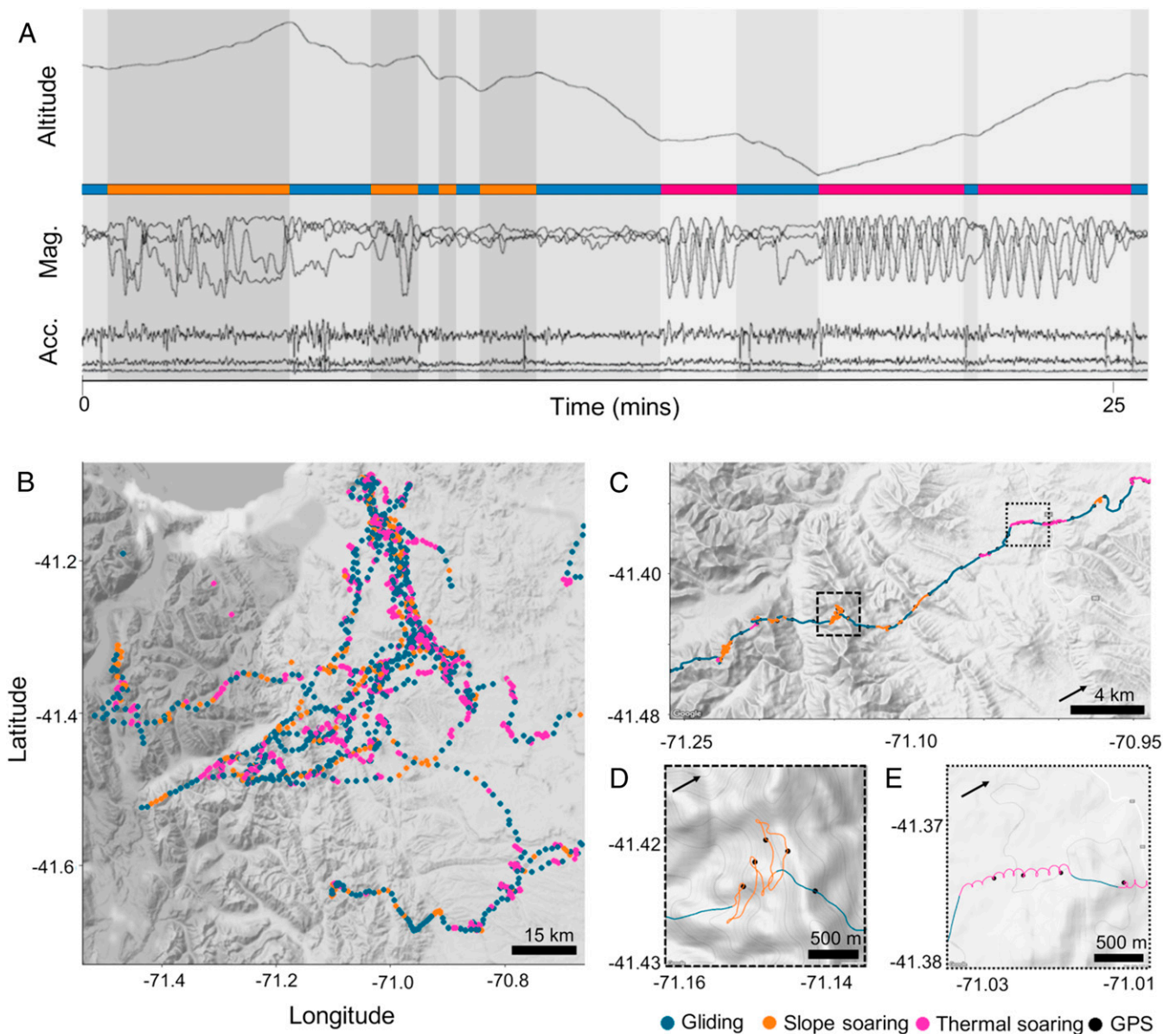
This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1907360117/-DCSupplemental>.

continuous data enable us to identify each and every wingbeat, from which we assess the precise conditions that elicit flapping. We hypothesized that flight costs would be linked to the prevailing conditions, decreasing with increased availability in updrafts stemming from wind speed and thermal convection (26, 27, 29). We thus expected to see a space-linked pattern of effort, with flapping flight less likely in more mountainous areas, which are associated with updrafts in a wide range of weather conditions. However, even in regions where updrafts tend to be strong, such as over mountainous terrain, soaring birds must contend with temporal and fine-scale spatial variation in the availability of rising air. In fact, mountains are characterized by particularly complex airflow regimes (30). Therefore, operating in these areas is in itself, a strategy that will ensure low movement costs. As a result, we examined the physical determinants of the investment in

flapping flight at two different scales: across all flight time and in the specific phases when condors were moving between sources of rising air (categorized as thermal updrafts or orographic updrafts in the case of slope soaring). Overall, our results reveal the capacity of these birds to soar and the environmental factors that may constrain the movements of large soaring fliers.

### Methods

Eight immature condors (9.5 to 13.9 kg) were each equipped with an archival "Daily Diary" (DD) unit (Wildbyte Technologies) (31), a GPS unit (Mobile Action Technology, model GT-120), and a miniature VHF in Bariloche, Argentina (a region of mountainous Andes and flatter steppe) from 2013 to 2018 (32) (*SI Appendix*). The DD loggers included a triaxial accelerometer (sampling at 20/40 Hz, enabling identification of wingbeats), a triaxial magnetometer (sampling at 40 Hz, enabling distinguishing circling in thermals from soaring in slope lift) (Fig. 1) (33, 34), and a barometric pressure



**Fig. 1.** The classification of passive flight types and their distribution in space. (A) Ethogram of flight types within a single flight, classified according to the rate of change in altitude (from pressure data, in Pa) and heading (from triaxial magnetometry; Mag, G), and the absence of flapping (dynamic movement in triaxial acceleration; Acc, g). (B) GPS points (60-s frequency) within the local region, color-coded by flight type. (C) The track of a single flight from the mountainous Andes to the steppe, resolved by dead-reckoning between GPS fixes (black circles) using the heading (from the magnetometer) and a constant speed. (D and E) Evidence of slope soaring in the dead-reckoned track, with the bird tacking back and forth up a slope (D) and thermal soaring, with the bird circling within the thermal (E).

sensor (sampled at 2/4 Hz and subsequently extrapolated and converted to altitude above sea level [ASL] and vertical velocity) (33). The GPS logger was programmed to sample once per minute. We analyzed ASL, rather than altitude above ground level (AGL), due to the higher recording frequency of barometric pressure compared with GPS data and increased error in calculating AGL (35). Tags were housed together in a unit representing ~1% of bird body mass. This was attached to the lower back using Tesa tape and programmed to release from the bird after  $\leq 10$  d using a release system based on the heating of nichrome wire looped through a stretch of fishing line.

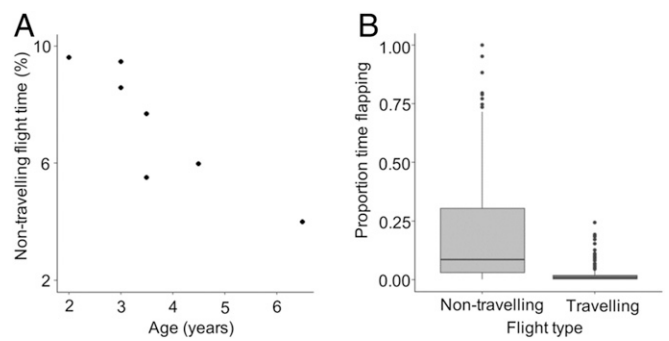
Takeoff periods, amount of flapping, and type of soaring behavior were recorded across flights (*SI Appendix, Fig. S1 and Table S1*), which were separated into two categories according to length (<10 min and >10 min). Flight effort was then modeled in the longer flights, which were likely to represent departures from roost or foraging sites. Here flight effort was quantified using a single metric derived from the acceleration data that increases with both the frequency and amplitude of the flapping signal: vectorial dynamic body acceleration (VeDBA) (36). Linear mixed-effects models were used to assess variation in flight effort (mean VeDBA per 10-s window) as a function of (i) flight altitude and wind speed, both in interaction with flight type (nonflapping flight, flapping, and takeoff), and (ii) habitat (tested by proxy using longitude to capture the changing topography between the Andes and the steppe, using a subset of data linked with GPS locations). Finally, we focused on specific flight behaviors ( $n = 6$  condors, due to sensor failure on 2 birds) to assess (iii) variation in takeoff effort as a function of altitude and whether or not birds had just fed (as indicated by activity and changes in pitch on the ground (*SI Appendix, Fig. S2*) (27), and (iv) whether the use of flapping flight in glides varied according to the type of updraft that birds were moving between. DD data were processed using custom-built DDMT software (Wildbytes; <http://wildbytetechologies.com/research.html>), and statistical analyses were performed in R version 3.5.1. More details are provided in *SI Appendix*. All experimental procedures were approved by the Swansea University Ethics Committee in 2010 (prior to the adoption of IP numbers) and by Universidad Nacional del Comahue.

## Results

A total of 235 h of flight time was recorded from eight Andean condors, mostly in long traveling flights ( $n = 226$ , representing >216 h and >1.3 billion data points). Individuals spent an average of 182 min  $d^{-1}$  traveling between roosting and feeding sites (maximum 11 h  $d^{-1}$ ). Much of this was spent patrolling a localized region in which domestic livestock were concentrated (Fig. 1 and *SI Appendix, Fig. S3*). The median flight distance in these flights was 17.6 km (interquartile range [IQR], 10.0 to 35.5 km), with a maximum of 306 km (estimated using the mean groundspeed of 9.1 m  $s^{-1}$ , taken from flights with 1-min GPS fixes). Birds spent 15 min  $d^{-1}$  in shorter flights ( $n = 449$  flights, total >18 h) (*SI Appendix, Table S2*). Younger birds spent a higher proportion of time in short flights, although the age range was relatively limited (Fig. 2A).

The incidence of flapping was remarkably low, representing 1.3% of all flight time, 0.8% of traveling flights, and 8.6% of short flights (Fig. 2B;  $n = 8$  birds) (*SI Appendix, Table S2*). The longest periods of uninterrupted, nonflapping flight ranged from 98 to 317 min per bird, with birds covering up to ~172 km in this time. The time spent flapping when traveling (mean, 4.4 min  $d^{-1}$ ) was driven by the use of powered flight in takeoff (mean, 3.3 min  $d^{-1}$ ; median, 8.9 s per flight, ranging up to 6 min). Flapping frequency was relatively consistent, with a mean frequency of ~2.7 Hz (*SI Appendix, Fig. S1*).

**Effort in Traveling Flight and Takeoff.** Altitude was the most important parameter determining overall flight effort (mean VeDBA), with greater flight effort occurring at low altitudes during both traveling flight and takeoff ( $\chi^2 = 37.10$ ,  $df = 9.2$ ,  $P < 0.001$ , marginal  $R^2 = 0.66$ , conditional  $R^2 = 0.72$ ) (*SI Appendix, Table S3*). While flight effort increased with wind speed ( $\chi^2 = 115.3$ ,  $df = 9.1$ ,  $P < 0.001$ , wind speed range, 4 to 47 km  $h^{-1}$ ) (*SI Appendix, Fig. S4*), wind explained little of the variance; the difference in marginal  $R^2$  values was 0.006. In addition, contrary to our predictions, topography



**Fig. 2.** Time spent flapping in nontraveling and traveling flights (<10 min and >10 min duration, respectively). (A) Younger birds spent more time in short, nontraveling flights (median = 89 s, IQR = 196 s per flight) relative to that spent in traveling flights (median = 1,943 s, IQR = 2,793 s per flight). (B) The proportion of time spent flapping was greater in nontraveling flights; flapping frequency was consistent across individuals and flight types at ~2.7 flaps  $s^{-1}$ .

(tested by proxy using longitude) was not a significant predictor of flight effort (random sample of  $n = 200$ ; Parameter estimate =  $-0.02$ ,  $df = 199$ ,  $t = -0.30$ ,  $P = 0.769$ , marginal  $R^2 = 0.66$ , conditional  $R^2 = 0.72$ ). Takeoff effort was predicted by altitude and feeding, with greater effort after feeding ( $n = 71$ ) than after periods of rest ( $n = 155$ ) ( $\chi^2 = 52.37$ ,  $df = 1$ ,  $P < 0.001$ ). There was no clear trend in takeoff effort with time of day (*SI Appendix, Fig. S5*) or with wind speed ( $P = 0.632$ ,  $r = 0.03$ ).

**Effort in Gliding Between Updrafts.** Birds spent over twice as much time soaring in thermals (32.5% of flight time) than in orographic uplift (12.1%;  $n = 6$  condors) (*SI Appendix, Fig. S5*). Perhaps surprisingly, the average positive vertical velocities were similar between the two categories, with a median of 1.67 m  $s^{-1}$  (IQR = 0.44) in thermal updrafts and 1.49 m  $s^{-1}$  (IQR = 0.32) in slope lift (as averaged across 10-s intervals). However, mean vertical velocities will be biased downward by the increased amount of time that birds have to spend when climbing in weaker updrafts. Indeed, maximum thermal climb rates were very high, as birds were able to sustain climb rates of up to 8.0 m  $s^{-1}$  (again averaged over 10 s).

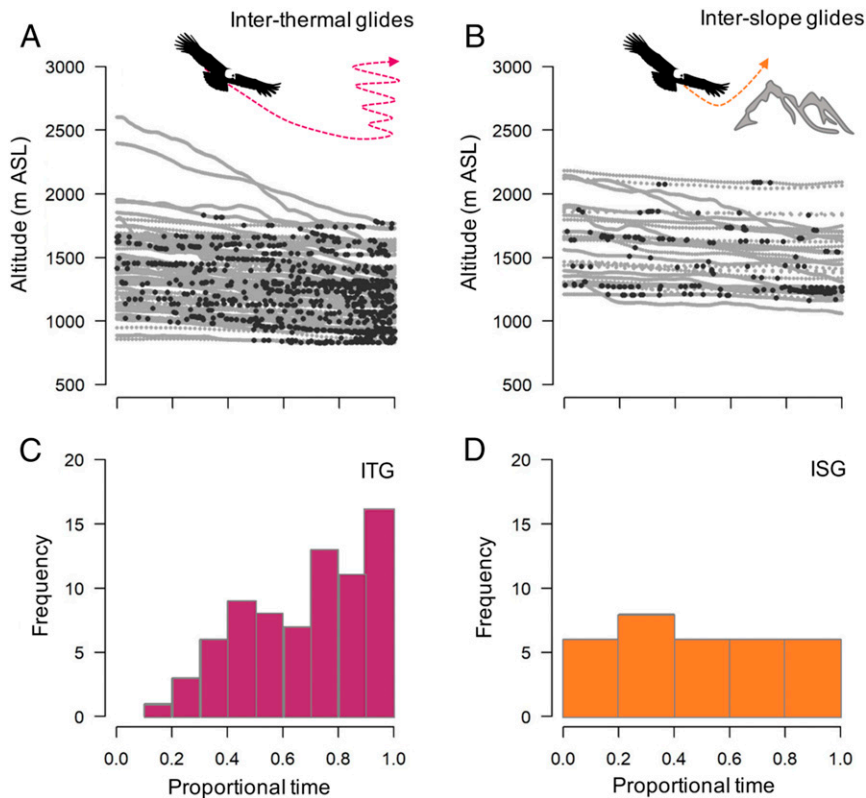
In total, 1,207 glides were identified, with birds moving between thermal updrafts ( $n = 639$ , median duration = 107 s, median altitude loss = 122 m) (*SI Appendix, Fig. S6*) and sources of slope lift ( $n = 568$ , median duration = 84 s, median altitude loss = 88 m). Flapping occurred more frequently in interthermal glides (ITGs; 15% of 639) than interslope glides (ISGs; 9% of 568;  $\chi^2 = 10.47$ ,  $df = 1$ ,  $P = 0.001$ ), and the number of seconds flapping was greater between thermals (median = 6 s, IQR = 1.5 to 11 s) than slopes (median = 2 s, IQR = 1 to 4 s;  $\chi^2 = 11.30$ ,  $df = 1$ ,  $P < 0.001$ , Kruskal–Wallis test). The likelihood of condors flapping in ITGs was not related to wind speed ( $t = 0.103$ ,  $df = 84.60$ ,  $P = 0.918$ ,  $n = 490$ ) but it did vary with the climb rate in the previous thermal, with flapping being more likely when birds were moving between weak thermals ( $t = 4.48$ ,  $df = 98.58$ ,  $P < 0.001$ ,  $n = 490$ ) (*SI Appendix, Fig. S7*).

The distribution of flapping within glides also differed according to the source of uplift that birds were moving toward. Flapping tended to occur ~70% of the way through ITGs (significantly different from bootstrapped random distributions,  $\bar{x}P < 0.001$ ) (Fig. 3), while the timing of flapping in ISGs did not differ from a random distribution ( $\bar{x}P = 0.578$ ).

## Discussion

Our data reveal the lowest levels of flapping flight recorded for any free-ranging bird, with condors remarkably spending 99% of





**Fig. 3.** The distribution of flapping in gliding flight. (A and B) Flapping (black data points) occurred more in ITGs ( $n = 99$  with flapping, 15% of all ITGs for the six condors) (A) than in ISGs ( $n = 52$  with flapping, 9% of all ISGs for the six condors) (B). (C and D) Flapping was also more likely near the end of glides between thermals than in glides between sources of slope lift. Time through the glide is given as proportional time, although there was no difference in glide duration for these flapping glides (median ITG = 120 s, ISG = 86 s;  $\chi^2 = 2.34$ ,  $df = 1$ ,  $P = 0.126$ ).

all flight time in soaring/gliding flight. Indeed, one bird remained airborne for  $>5$  h without using flapping flight, covering  $>170$  km. The extraordinary low investment in flapping flight was seen in all individuals, which is notable, as none were adult birds. Therefore, even relatively inexperienced birds operate for hours with a minimal need to flap. Nonetheless, the flap rates reported here for condors may represent the lowest that are achievable for this age range, as the amount of flapping flight was dominated by the effort required to get airborne (11, 37), which did not vary with flight conditions. Furthermore, conditions for traveling in our study were at a seasonal peak due to maximum thermal convection and strong winds (25). As a result, birds were not limited by the availability of one or the other source of updraft, but could soar readily to and within their feeding grounds, with no change in flight effort as they moved further from the Andes. Thus, the marked easterly limit to the condors' range (38) may be driven by an interaction between food availability and flight costs rather than by flight costs alone. For instance, the physical environment could affect the number of hours in which these birds can operate per day with minimal costs (25), rather than the costs per unit of time.

The condor's ability to forage almost entirely without flapping is notable (28) given that all inferences about how the largest extinct animals flew (24, 39) assume that flight was possible only due to an extreme reliance on soaring. Lighter species appear to use flapping flight to a much greater extent than condors, with white storks (*Ciconia ciconia*,  $\sim 3$  kg) and ospreys (*Pandion haliaetus*,  $\sim 1.6$  kg) flapping for 17% and 25% of their over-land migratory flights, respectively (40, 41). Interestingly, the wandering albatross (*Diomedea exulans*;  $\sim 9.4$  kg), which in many ways

might be considered the condor's marine counterpart due to its body size and reliance on subsidized flight, spends 1.2 to 14.5% of its flight (outside takeoff) in slow, flapping flight (39). The costs of slow flapping flight may differ between the two systems, although relative costs of flapping cannot be directly compared without information on wingbeat amplitude. Nonetheless, the difference is intriguing, as it suggests that the use of flapping flight may also vary with soaring strategy.

The magnitude of takeoff costs in condors demonstrates the consequences of errors in judgment during soaring-gliding flight, as a single extra landing could substantially impact the overall flight budget due to the effort required in the subsequent takeoff. For instance, while flapping flight constituted 1% of condor flight time, it represented an estimated 21% of the daily flight costs, with the energy required for 3.3 min of flapping in takeoff being equivalent to that used in 50 min of soaring, taking the cost of flapping to be 30 times the resting metabolic rate (RMR) (22) and the cost of soaring to be twice the RMR (18–20), based on RMR estimates from Benedict and Fox (42). This, and the strong relationship between takeoff effort and altitude, suggests that condors should be very selective about where they land. In our study area, condors currently feed on carcasses of domesticated livestock reared in the relatively low steppe (25, 38). Historically, condors would have patrolled the same regions, in which domesticated livestock have replaced large herds of native herbivores, such as guanacos (*Lama guanicoe*) (38). We know from the placement of experimental carcasses (43) that condors will not land in all locations, and indeed, once on the ground, condors are vulnerable to predation and disturbance from terrestrial mammals (43, 44). This suggests that while condors

operate in a landscape that is rich in opportunities for low-cost flight, there is little room for error when flying close to the ground. This puts these large birds in a unique category in which the costs of flapping flight are extremely high but, almost analogous to frigatebirds (45), they are not free to land in all areas.

The risk of grounding likely explains why condors were more likely to flap toward the end of interthermal glides (assuming that distance to the ground decreases through the glide, as is evident in the subset of glides for which both GPS and pressure data were recorded at high frequency; *SI Appendix, Fig. S6*). As condors flapped more in the early mornings, when both thermals and the surrounding downdrafts are weak, it is unlikely that their use of powered flight represents a response to sinking air (28) or the need to increase flight control in response to turbulence (46). Indeed, the pattern of flapping suggests that condors use powered flight to try and stay airborne while they find the next thermal updraft, with the alternative being to risk grounding.

This raises the question of why individuals leave thermals with insufficient height to get them to the next thermal without flapping. Given that birds use more powered flight in glides when thermals are weak and shallow (47), condors are likely to have climbed in these thermals for as long as they were able. Consequently, the use of powered flight might not indicate an error in judgment in the patch-leaving decision. Instead, we propose that temporal variation in thermal activity forces birds to switch to powered flight. Even if a bird moves toward an area that tends to be associated with thermal activity, air might not be rising at the specific moment the bird needs it [as shown in figure 1 of Shepard et al. (48)]. Furthermore, periods of thermal inactivity may be longer when convection is weaker. This contrasts with the availability of orographic lift, which should be much more predictable in space and time, being associated with windward slopes even at relatively low wind speeds. The difference in predictability between updraft types is supported by the fact that birds flapped more when moving toward thermals, and that flaps occurred toward the end of the glides rather than at random intervals, as seen when flying to slope lift.

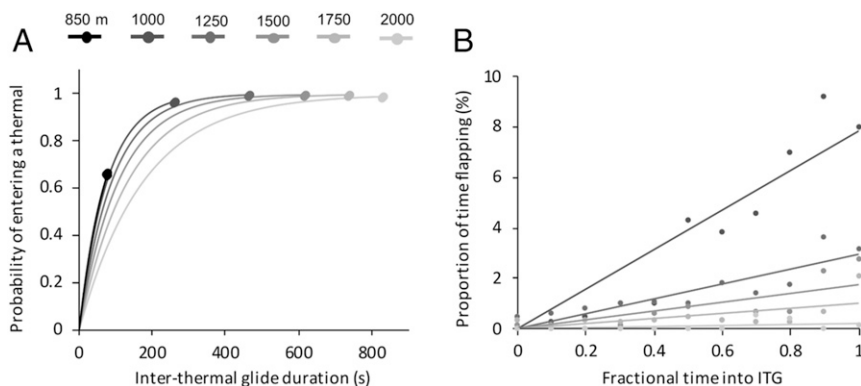
The suggestion that there is an energetic cost associated with thermal “hotspots” not always being “hot” is an example of how animals can provide insight into the behavior of the physical resources that they exploit. Very little is known about thermals at the fine scale, but there is increasing interest in programming autonomous vehicles to operate in a similar manner to birds (49). Yet neither birds nor unmanned aerial vehicles can detect thermals at a distance unless they are being exploited by other animals/vehicles (50), transporting particulate matter, or marked

by cloud development. As a result, both types of flier must “gamble” when moving between sources of uplift.

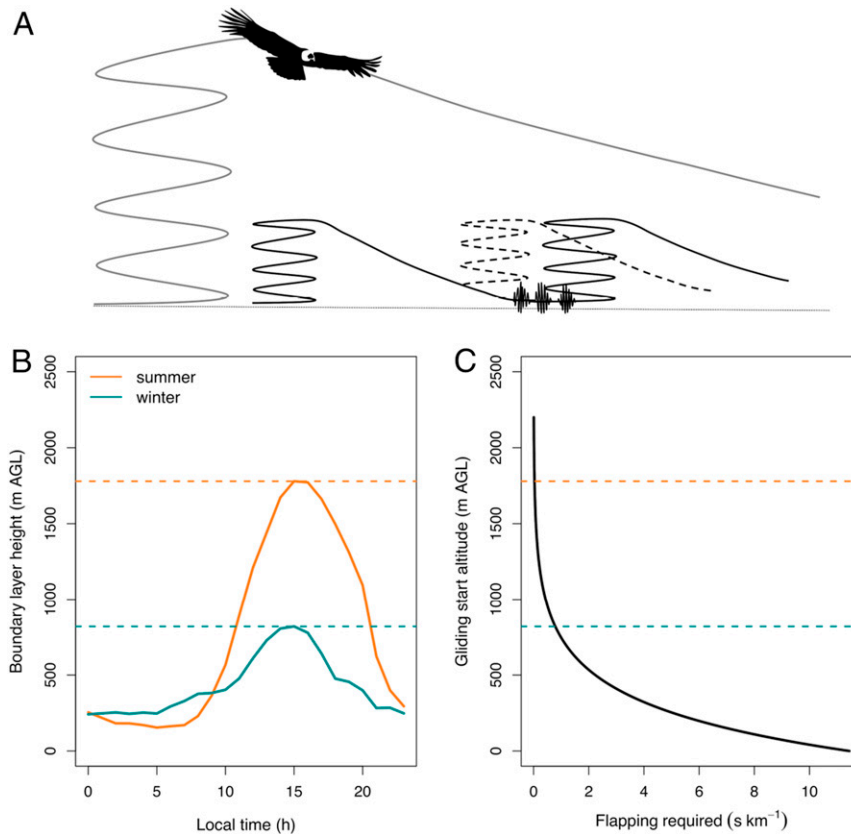
The risks of not encountering a thermal before reaching the ground diminish with sufficient height (Fig. 4A). In fact, converting the glide durations into the probability of thermal encounter (*SI Appendix, Fig. S8*) demonstrates how the probability of encountering a thermal declines at lower leaving altitudes, so that if a bird leaves a thermal at  $\leq 1,000$  m, it must invest energy to extend the glide duration (Fig. 4B). The scale of these costs should show seasonal variation, with a reduction in insolation in winter leading to a decline in soaring height, with the need to find more thermals to cover a given distance. We modeled this, using our data to relate time spent flapping with the height that a condor left a thermal, and then converted this to time spent flapping per km using the mean interthermal glide speed (Fig. 5). Our predictions show that changes in thermal height could lead to a twofold to fourfold increase in the effort required to move between thermals in winter (Fig. 5C); however, this may still lead to a relatively small increase in overall flight effort due to the extraordinarily low investment in flapping outside takeoff.

It is difficult to predict how takeoff costs will vary seasonally (or indeed with global change), but the number of landings and subsequent takeoffs should be influenced by food availability. During winter, cold temperatures may lead to higher herbivore mortality (51, 52). A winter increase in food supply may offset the costs of low insolation and low wind strength, and may explain how condors can operate in the same region year-round without undertaking seasonal migrations or altering the general pattern of their daily flights (32). In fact, we predict that winter may be less costly than autumn, when thermal convection is frequently shut down by rain and fog. These conditions should be most challenging for younger birds, which spent more time flapping in short flights (Fig. 2), suggesting that their flight inexperience and/or low dominance rank levies a metabolic cost, either by flying near the roost before conditions support soaring or by being displaced from perches and/or carcasses. Furthermore, they will be less able to support these costs, given that their position in the dominance hierarchy (53) may force them to make more landings to obtain a given amount of food.

Overall, therefore, the remarkably low investment in flapping flight in the largest soaring birds was limited by the need to take off. The minimal amount of flapping is only partly explained by the season of our study, as we predict that birds should need to flap for only roughly 2 s per kilometer when thermal-soaring in winter (Fig. 5C). Nonetheless, we note that our results relate to movement within a restricted longitudinal range, and it is unclear how flight effort would vary outside this, potentially affecting the



**Fig. 4.** The probability that flapping is required to reach the next usable thermal. (A) The probability of finding a usable thermal without flapping increases with time spent gliding away from the previous thermal according to starting altitude. Each curve reaches a maximum by the time birds reach ground level (800 m ASL) derived using our relationship between sink rate ( $V_z$  [in  $\text{m s}^{-1}$ ]) and altitude ( $A$  [in m]) ( $V_z = 0.697 - 0.001693 \cdot A$ ). (B) The proportion of time dedicated to flapping (in those glides with flapping) decreases as a function of starting altitude ( $n = 459$  glides grouped by starting altitude at 1,000 to 2,000 m ASL).



**Fig. 5.** Daily and seasonal changes in the cost of thermal soaring. (A) Summary of the relationships between thermal strength, leaving altitude, and the likelihood birds will need to flap. Birds should not invest energy in flapping if the probability of finding a thermal is still appreciable, i.e., at high leaving altitudes (solid gray trajectory). In poor conditions, condors leave at lower altitudes (solid black line) and require a greater number of thermals per unit distance. Birds can increase their time aloft (if they have not yet reached a thermal; dashed line) by limited flapping toward the end of the glide (indicated by intermittent acceleration peaks; solid black trajectory). (B) Seasonal changes in the costs of moving between thermals modeled using hourly boundary layer heights (for Bariloche: EMCWF forecast data, <https://cds.climate.copernicus.eu/>) as a proxy for maximum altitudes attainable in thermal soaring; midsummer and midwinter are taken using data from January and July, respectively, for 2015 to 2018). These heights (AGL) increase throughout the day, peaking at 15:00 (midsummer  $\bar{x}$  = 1,780 m; midwinter  $\bar{x}$  = 960 m), but are generally lower in winter. (C) Condors are predicted to flap more to cover a given distance in the winter, as derived using the proportion of time birds flapped in the glides and the average groundspeed in gliding, 13.56 m s<sup>-1</sup>.

scope for exploiting such areas. Furthermore, birds are likely to modulate their use of flapping flight by simply choosing to not fly in suboptimal conditions. Investigation of the specific times and conditions when condors do not fly is needed to further assess the relationship between the weather and condor flight effort. This type of approach, using whole-animal performance (54) is likely necessary to provide insight into the nexus of morphological and environmental constraints experienced by large fliers, the potential effects of global change on the energy expenditure of those species, and how this translates into patterns of space-use.

**Data Availability.** GPS and biologging data for the eight condors have been uploaded to Movebank ([https://www.movebank.org/cms/webapp?gw\\_fragment=page=studies,path=study1109284853](https://www.movebank.org/cms/webapp?gw_fragment=page=studies,path=study1109284853)) under

the study “Andean Condor (*Vultur gryphus*), Immatures, Bariloche, Argentina, 2013–2018.”

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