

LETTER

Turn costs change the value of animal search paths

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Abstract

The tortuosity of the track taken by an animal searching for food profoundly affects search efficiency, which should be optimised to maximise net energy gain. Models examining this generally describe movement as a series of straight steps interspaced by turns, and implicitly assume no turn costs. We used both empirical- and modelling-based approaches to show that the energetic costs for turns in both terrestrial and aerial locomotion are substantial, which calls into question the value of conventional movement models such as correlated random walk or Lévy walk for assessing optimum path types. We show how, because straight-line travel is energetically most efficient, search strategies should favour constrained turn angles, with uninformed foragers continuing in straight lines unless the potential benefits of turning offset the cost.

Keywords

Brownian motion, correlated random walk, energetics, Lévy walk, movement costs, search strategy, turn angle, turn radius.

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INTRODUCTION

A prime driver behind animal movement is the acquisition of resources (Pyke 1984) where the form of the track taken with respect to the distribution of the food will profoundly affect foraging success (Pearce-Duvel *et al.* 2011). This premise has led to burgeoning studies examining the value of particular movement strategies, such as Brownian motion, Correlated Random Walk and Lévy walk, with respect to maximising prey encounters with variously distributed food sources (Viswanathan *et al.* 2008; Schlesinger 2009). Optimal foraging theory predicts that movement strategies should result in animals maximising the net gain of the resource, usually energy (Stephens *et al.* 2007). Yet while this specifically requires energy expenditure to be pitted against energy acquisition, movement strategy studies rarely consider how energy expenditure might relate to the details of the movement (Shepard *et al.* 2009). Instead, they implicitly assume the rate of energy expenditure during search to be constant, a concept supported by studies showing how animals often search for food at a constant (and lowest possible) cost of transport (Culik *et al.* 1994). Typically, therefore, the perceived cost of movement, which is commonly described by variable step lengths interspaced by turns (Bartumeus *et al.* 2005), using poorly resolved data compared to the turn radius of animals, is quantified by simply summing step lengths over time between prey encounters as a linear proxy for cost (Schmidt-Nielsen 1972). This ignores any cost associated with the turns, implicitly assuming them to be negligible. Given that the frequency and extent of turns are pivotal in describing search strategy (Janson & Di Bitetti 1997; Vasquez *et al.* 2002), their cost should be investigated explicitly. Newton's first law of motion states that the velocity of a body will be constant unless acted upon by an external force, implying that, in a homogeneous energy landscape (*sensu* Wilson *et al.* 2012), all

animals require extra energy to turn, whether terrestrial, volant or aquatic (e.g. Usherwood *et al.* 2011). On the basis of this, we hypothesise that, unless animals can use environmentally provided energy (cf. Shepard *et al.* in press), turns within movement paths will constitute an appreciable cost for movement strategies, with costs escalating with increasing frequency and extent of turns. In this work, we examine this by measuring turn costs in a terrestrial animal and modelling them in a flying animal, before considering the implications these costs have for our understanding of optimisation of all animal movement strategies.

MATERIALS AND METHODS

Measurement of the costs of turns in humans

Empirical data on the costs of turning in a terrestrial mammal were collected using 10 human participants. They were equipped with a portable respirometer (Oxycon mobile, Viasys, Germany) for measuring rate of oxygen consumption, walking at a fixed speed on a standard surface, interspacing defined straight stretches traced on the ground, with turns of specified angles, with equal numbers of left- and right-hand turns. There was no prescribed protocol for the turns, which took a negligible time compared to the walking between turn phases and appeared virtually instantaneous. Each participant undertook 5 walking and turning conditions, randomly assigned in order, each of which consisted of 5 m straight walking stretches interspaced with prescribed turns corresponding to 0, 45, 90, 135 or 180°, according to condition number. Speed was maintained constant [at 1.67 m s⁻¹ (cf. Witte & Wilson 2004)] using a digital, auditory metronome to sound once half-way between turns and once on turns. All participants continued in each trial until rate of oxygen consumption ($\dot{V}O_2$) had stabilised for at least 60 s

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(usually after 3 min). Mean $\dot{V}O_2$ values defining energy expenditure for each trial were taken from the last 60 s.

Derivation of the costs of turning in a flying animal

The metabolic cost of flight is problematic to measure directly but conceptual design models for aircraft have powerful predictive capacity (Anderson 2008; Pennycuik 2008). Specifically, the energy required for a turn (above that of straight and level flight) can be derived from the increase in drag that would result if a flying animal were to maintain altitude and speed while banking. We adopted this approach using a gliding bird, the Andean condor *Vultur gryphus*, as our model. Thus, this approach first calculated the lift and the drag of a condor travelling in a straight line in terms of its speed and wing area. The increase in lift necessary to correct for the angled wings during a banked turn of defined radius was then calculated and this increased lift was then defined by the resultant increased drag on the bird. Finally, from this, we derived the increased energy necessary to compensate for it (see supplementary information).

Costs of transport in defined movement types

We used the information on the cost of turning from our flying model to examine its effect on the cost of movement in a correlated random walk (CRW), a diffusive movement model that nicely represents random search patterns by many animals, where the previous step direction influences the direction of the following step (e.g. Dickson *et al.* 2005 and refs therein). First, we subjected CRW with fixed step lengths to increasingly constrained turn angles between steps to examine how turn angle related to power use and the cost of transport, deriving mean values from 100 runs per scenario. Second, we created two cases of CRW, each case with the same diffusion D coefficient and overall distances travelled, but one case consisting of short steps and small turns and another with long steps and large turns, to compare power use and costs of transport for the two scenarios. As CRWs are diffusive walks (for correlation $r < 1$), the expected net squared displacement from the starting point after a given time T is asymptotically equal to $4DT$. The diffusion coefficient D is related to path sinuosity S and mean movement speed V by: $D = V/S^2$ (Benhamou 2006). When V does not vary across CRWs, then D only depends on S , which is a combination of step lengths and turn distribution parameters (Benhamou 2004):

$$S = 2 \left[E(l) \left(\frac{1 - c^2 - s^2}{(1 - c)^2 + s^2} + b^2 \right) \right]^{-0.5} \quad (1)$$

where $E(l)$ is the mean step length, b is the coefficient of variation of step length, and c and s are the mean cosine and sine of turns respectively (the directional correlation is given by $r = (c^2 + s^2)^{0.5}$). When right and left turns are balanced ($s = 0$) and the step length is constant ($E(l) = p$, $b = 0$), S becomes:

$$S = 2 \left[p \left(\frac{1 + c}{1 - c} \right) \right]^{-0.5} \quad (2)$$

In this framework, it is therefore easy to design CRWs with quite different step lengths and mean cosine of turns, but showing the same sinuosity and thereby the same diffusion coefficient. For instance, if the step length of a CRW with mean cosine of turns c is

taken as p_c , a non-correlated RW (CRW with $c = 0$ i.e. constant discrete step Brownian motion) can be designed with the same sinuosity (and diffusion) by setting: $P_0 = p_c(1 + c)/(1 - c)$. Note that in the more usual case, where step length is not constant (cf. Codling *et al.* 2008) but is drawn from an exponential law with mean $E(l)$ ($b = 1$), one gets $E(l)_0 = E(l)_c/(1 - c)$.

Costs of transport in an example soaring bird

We used data from a GPS-corrected, dead-reckoned condor track where bird positional data were calculated at subsecond resolution by interpolating between GPS-fixes (at 11 s intervals) using an on-board compass to derive bird heading (see Shepard *et al.* 2011). Our positional data were thus described by points separated by 0.17 s in time which, at a flight speed of ca. 15 m s^{-1} (Shepard *et al.* 2011), equates to straight-line sections of $\sim 2.5 \text{ m}$ (about twice the length of an Andean condor and unlikely to incorporate more than a small fraction of a turn), which we progressively decreased in resolution by increasing the time intervals for positional fixes to one fix every 83 s. We then used the values predicted from our flight model (see above) to calculate the power used and the cost of transport (COT) incurred during the track in relation to the different step lengths to have an explicit test of the above phenomena in a wild animal.

RESULTS

The empirical data on humans showed that turn costs are substantial and are linearly related to turn angle (Fig. 1). These results imply that a single 180° turn cost the same as walking at 1.67 m s^{-1} for 5.88 m in a straight line. Although greater extents of turns were clearly related to higher oxygen consumption, it was not clear how the angular velocity of turns varied with turn angle and whether angular velocity, which was most likely to have been higher in the more substantive turns, contributed to the costs of turning. The modelled bird results showed similar trends, with energy consumption being 2.58 J° of turn over and above that required for straight line travel. In this latter case, a 180° turn equated to 20.7 m of

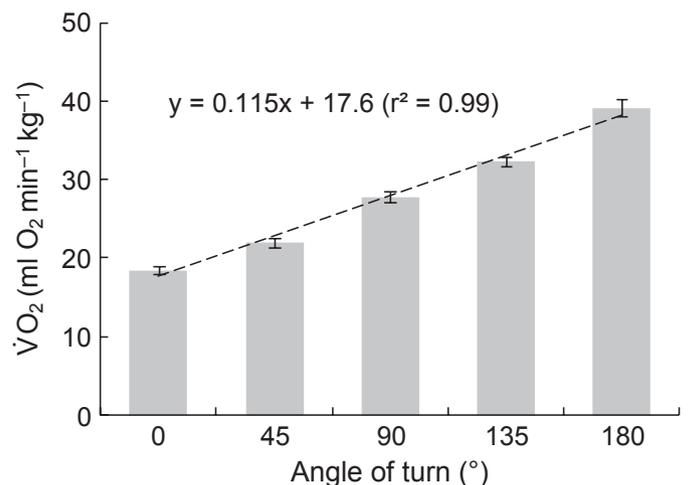


Figure 1 Oxygen consumption in humans (+ SEM) during walking and turning as a function of turn angle. The gradient of the regression represents the costs of turning since both walking speed and distance between turns are constant.

straight line travel (assuming a turn radius of 27.8 m and a glide speed of 16.5 m s^{-1}).

These turn costs markedly affected the cost of movement in theoretical random walks. Any turns increased costs of transport, with greater turn angles being resulting in greater costs of transport (Fig. 2) and the costs of transport increased overall with decreasing step length (Fig. 2). Our two cases of CRW for both humans and birds with simulated equivalent diffusion rates (diffusion distance was approximately equal between Brownian motion ($\pm 180^\circ$) at a step size of 1, and a correlated random walk ($\pm 18^\circ$) at a step size of 0.008) had power uses and COTs that were *c.* 96 and 143 times higher with high turn frequency than with low turn frequency, respectively, for both the human and bird.

Finally, the high resolution data (measurement intervals of 0.17 s) of the extended flight track (72 min) of a free-living Andean condor clearly showed the changes in flight trajectory associated with the exploitation of thermals where birds gain height (Shepard *et al.* 2011), although this was not obvious in the low resolution data (measurement intervals of 83 s; Fig. 3). The resolution of position played an important role in defining apparent movement costs (Fig. 3). As temporal resolution of step length decreased from 0.17 to 83 s, the apparent distance travelled decreased from 43.3 to 28.1 km (a 1.5-fold difference) and the total angle turned (the sum of all turns) decreased from 4923 to 55 radians (a difference of 89-fold; Fig. 3c). Both have implications for derived values of transport costs with the consequence being that the apparent power use decreased from 62.54 to 36.11 W kg^{-1} , while COT decreased from 3.7 to $2.14 \text{ J kg}^{-1} \text{ m}^{-1}$ (both representing a 1.7-fold difference; Fig. 3d). Turn angles displayed by the condor during its flight had a clear mode in the bin of $0\text{--}10^\circ$ (Fig. 4), although virtually all turn angles in excess of 60° were associated with the exploitation of

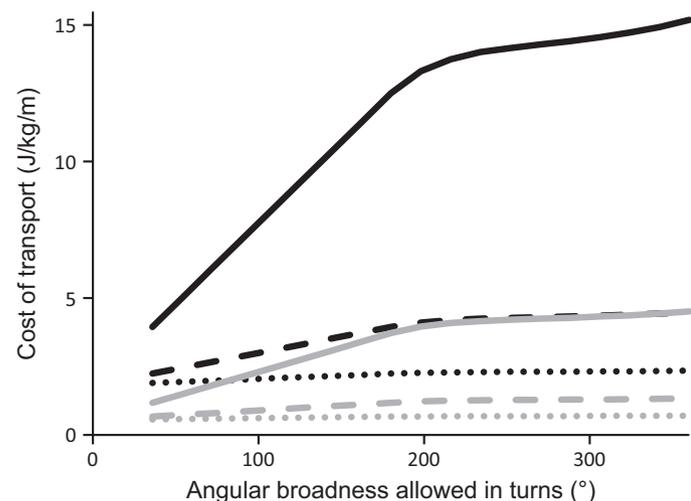


Figure 2 Mass-specific cost of transport (COT) as a function of increasing angles allowed in turns (in 16° increments) for derived correlated random walks executed by a walking human (black lines) and an Andean condor (grey lines) with varying step lengths (1, 5 and 25 m between turns, represented by continuous, dashed and dotted lines, respectively). For the bird, energy values were derived from a model (see text) while human values were derived empirically (see text). In the latter case, the conversion from oxygen consumption (see Fig. 1) to energy was taken to be $1 \text{ L O}_2 \equiv 20.92 \text{ kJ}$ (Franks B, Howley ET (1998) *Fitness Leader's Handbook*. Champaign: Human Kinetics Publishers).

thermals, and therefore gain in potential energy (Fig. 4) (Shepard *et al.* 2011). There was no such apparent advantage for turns at angles of less than 60° (Fig. 4).

DISCUSSION

This work demonstrates unequivocally that the costs for turning constitute an appreciable fraction of animal movement costs. Newton's first law of motion, noting that the velocity of a body will not change unless subject to an external force, indicates why this is so. Two factors may explain the general disregard for this among biologists: One is that there are occasions where animals may turn without investing energy because there is external energy from the environment, such as a downward slope or rising air (see Shepard *et al.* in press for a synthesis of this). Indeed, animals, especially flying birds which operate in a particularly variable energy landscape, presumably balance the costs of straight-line travel and turning with minimised costs of travel according to the availability of external, environmental energy (Shepard *et al.* in press). Second, that determination of animal movement costs, which is conventionally undertaken using gas respirometry on subjects on a treadmill (e.g. Halsey *et al.* 2009) or in a water flume (e.g. Wikelski & Cooke 2006), is challenging enough without considering a protocol that somehow incorporates turns. Carefully constructed experiments using gas respirometry on animals in a maze may provide a methodology, as may, e.g. heart rate metrics from logger-equipped wild animals (cf. Green *et al.* 2009) where turns can be resolved at fine scale. Similarly, in gliding birds such as the condor, logged data on turn angle can be examined with respect to sink rate in still air to derive loss of potential energy values. Currently, however, to our knowledge, only one study has ever explicitly documented turn costs, that of Minetti *et al.* (2011), who found that 15% of the costs of athletes running up skyscrapers was attributable to stairwell turns, although some studies, such as that of Usherwood *et al.* (2011) consider turn costs to be substantial.

Movement is pivotal in defining the way animals operate, and incorporation of turn costs should help explain patterns of movement-related phenomena from time scales ranging from seconds to lifetimes. Turn costs may help clarify, for example, why small prey pursued by large predators, such as gazelle fleeing from cheetah, tend to use sharp turns (Cooke 2008) while large prey fleeing from multiple small predators, such as some baleen whales from killer whales, or moose from wolves, appear to try and outrun them (Saunders *et al.* 1993; Handcock *et al.* 2009). At larger scales, incorporation of turn costs within models of animal search strategies will profoundly affect what is considered to be energetically optimal. Indeed, although our work does not attempt to relate movement costs to gain (such as energy gain in food) or to the energy landscape (Shepard *et al.* in press), it does show that overall movement costs depend on the scale at which movement is considered, with power use and costs of transport tending to increase with finer resolution of movement, irrespective of whether that movement is model based (Fig. 2), or derived from wild animals (Fig. 3). Thus, particular movement strategies, such as Lévy walk, which are considered scale invariant (Viswanathan *et al.* 1996), cannot be considered for optimality with regard to net energy return (Viswanathan *et al.* 2008) unless the step resolution allows for the sum of the calculated angles within the track to approach the real angular sum. This premise is acceptable since the costs for turns are a linear

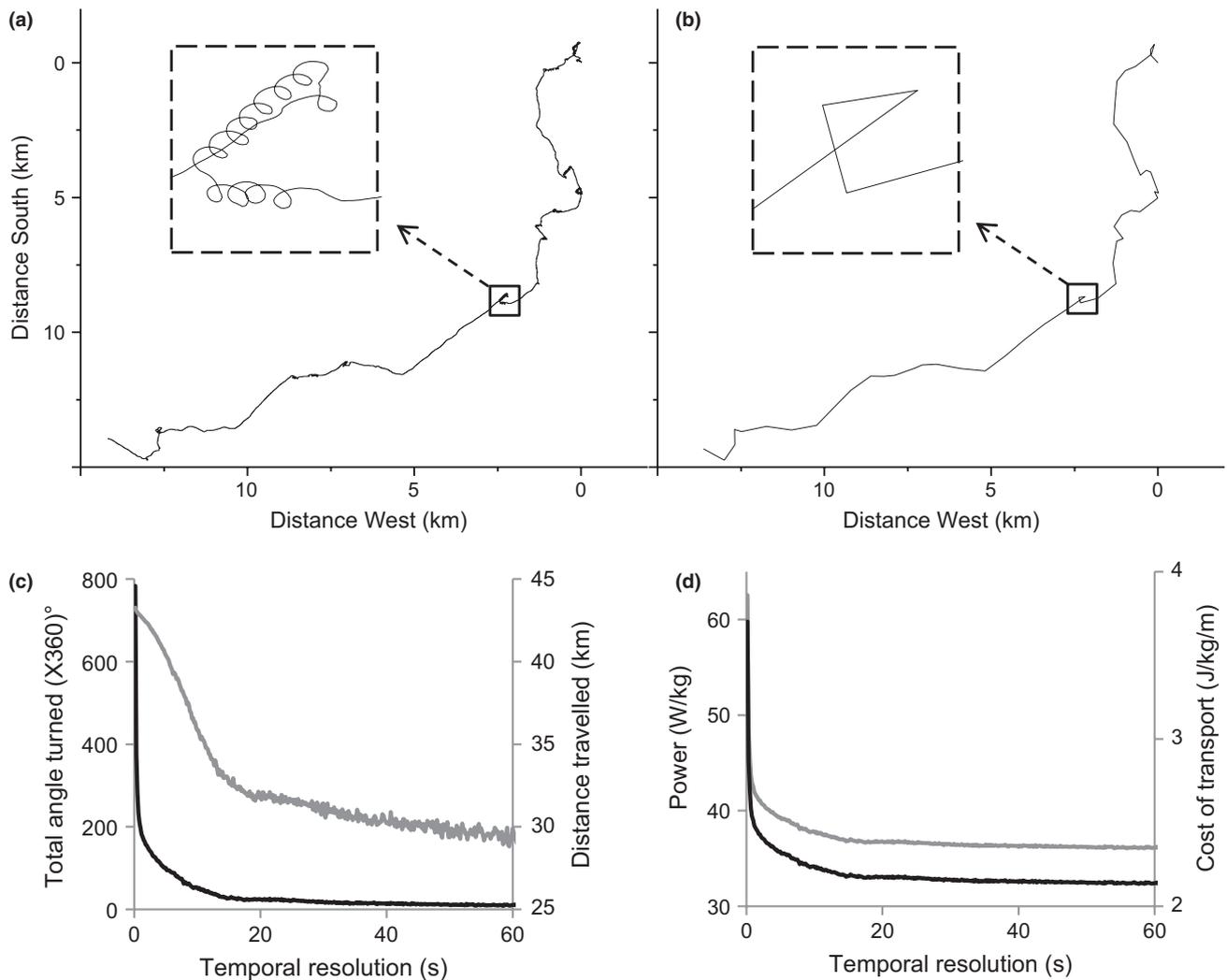


Figure 3 The movement of a free-living Andean condor during a 72 min flight exemplified by different time resolutions of the path, at intervals of (a) at 0.17 s and (b) 83 s. Insets show how the fine detail of the track, such as circling in thermals, is lost. (c) shows the calculated distance travelled (grey line) and the total angle turned (black line) as a function of the temporal resolution of the track while (d) shows the calculated power requirements (grey line) and costs of transport (black line). Note how both the apparent distance travelled and total angle turned decrease with decreasing resolution although there are marked differences in the relative change between them which account for the patterns observed in power and cost of transport.

function of turn angle (Fig. 1). In fact, an important outcome of this work is the finding that it is clearly not enough to consider step length distributions and random turn angles between steps as measures of animal search patterns (Ramos-Fernández *et al.* 2004). Rather, workers should explicitly determine the distribution of turn angles between steps (Ramos-Fernández *et al.* 2004) to enable strategy-based costs to be determined, and to determine associations between turn angles and step length to help understand why animals exhibit the patterns they do.

We suggest that animal turning be viewed within the same context as any other behaviour within an optimised framework and that moving animals should only incur the extra costs that turning incurs if the benefits for so doing outweigh them. Thus, foraging animals should only turn if this increases the probability that they will find food relative to the straight line strategy. More acute turns would indicate more compelling reasons to execute the turn, based on information, so that such acute turns would tend to be clustered in time and space, as we observed in the condor track. Indeed, exami-

nation of the extent to which turn angles are clumped may help researchers identify areas of interest (Weimerskirch *et al.* 2007), something that is very different from the supposed random turn angle premise applied at the end of each defined step in many modelled movement scenarios (Viswanathan *et al.* 1999; Bartumeus *et al.* 2005).

Authors considering movement patterns are generally constrained to work with positional data from animals at rather coarse spatial scales (e.g. Viswanathan *et al.* 2008), where step lengths are a convenience for quantifying movement between defined positions, irrespective of the track tortuosity between positions. Our work points to the dangers in this and even implies that fine-scale resolution of animal movement may reveal straight-line tracks, punctuated by turns based on decisions where animal-based energy costs of the turn are outweighed by the gains, such as increased likelihood of acquisition of food, or that external, environmental energy may diminish, negate or even reduce energetic costs, such as occurs in condors exploiting thermals (Shepard *et al.* 2011). Recent technolog-

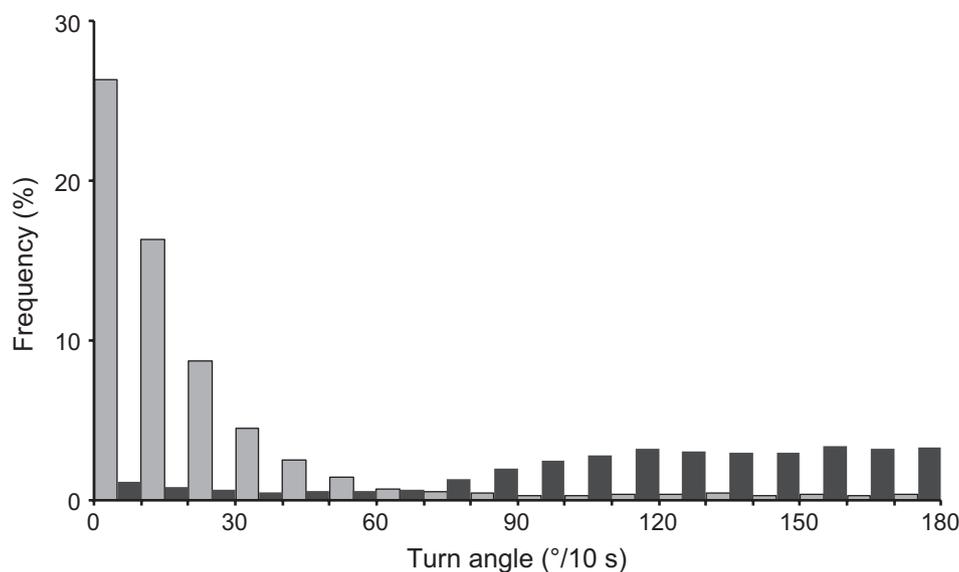


Figure 4 The frequency of turn angles for a single Andean condor flight of 72 min. The bird sometimes gained altitude by circling in thermal updrafts (series indicated in black). Such times were typified by high angular changes as the bird gained an energy resource (here potential energy) (Shepard *et al.* 2011), in contrast to the relatively straight glides between thermals (series in grey) where altitude was lost.

ical innovations (e.g. Wilson *et al.* 2008) will clarify this shortly. In the meantime, we suggest that, in contrast to viewing, e.g. Brownian motion, CRW or Lévy walk as fundamental search strategies for foraging animals (e.g. Van Hensbergen & Martin 1993; Mårell *et al.* 2002; Sims *et al.* 2008), they are actually an emergent property as a result of decisions to turn at particular times based on sensory or memory-based information (Moore & Kennedy 1985). The greater question might be how the hierarchy of information available to foraging animals, primarily through sensory systems (Hays *et al.* 2003; Nevitt 2008), leads to the patterns we observe. Indeed, we predict that future work adopting this approach will be able to marry the concept that animals react to their environment better using a series of biologically meaningful rules to apparent movement models rather than assuming that somehow animals adopt such models as a general solution.

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AUTHORSHIP AND CONFLICT OF INTEREST

The authors declare no conflict of interest. RPW and ELCS conceived the study, IWG and MIF provided the theoretical work, LGH ran the tests on humans and the analysis of the consequent data with RPW and ORB, PAL conducted the modelling with

IWG. SAL and ELCS provided data and all authors contributed to writing the manuscript.

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