

Frigatebirds ride high on thermals

This bird's bizarre physique and sparse hunting grounds account for its languid lifestyle.

Aspects of the morphology and life history of frigatebirds verge on the extreme, and how they spend their time at sea has been a mystery until now¹⁻³. Here we use data collected by altimeters and satellite transmitters attached to individual frigatebirds to show that these birds are continuously on the wing, day and night — they fly in a succession of climbs and descents, soaring in circles on thermals to heights of up to 2,500 m and gliding down in the direction of travel. The birds' curious morphology and flight patterns result in extremely low costs of foraging, but they also cause them to travel slowly over large distances, putting frigatebirds at an evolutionary extreme that enables them to exploit tropical waters in which prey is scarce.

Frigatebirds (Fig. 1) are designed for an aerial life, having the lowest wing-loading (that is, a relatively large wing area for a low body mass) of any bird and an inability to land on water⁴. Because of their particular morphology, it has been suggested that these sea birds have evolved specific flight strategies to exploit scattered food resources at low cost^{2,3}.

In April 2002, we investigated the vertical and horizontal movements of magnificent frigatebirds (*Fregata magnificens*; Fig. 1) while they were foraging at sea during egg incubation or chick brooding on the nature reserve of Grand Connétable, off the coast of French Guiana in the Atlantic Ocean. To record the birds' altitudes, we fitted seven adults (mass, 1.2–1.5 kg) with continuously recording altimeters (35 g; Suunto Oy; resolution, 3.3 m). We corrected the altimetric data for shifts in atmospheric pressure through recordings taken using a fixed altimeter in the colony.

To record the birds' horizontal move-

ments, we fitted eight individuals with Argos satellite transmitters (Microwave; PTT-100 solar- and battery-powered instruments, 18 and 32 g, respectively) for a total of 42 foraging trips lasting 8.4–93.8 h; loggers and transmitters were taped to the back feathers.

Altimeter readings indicated that frigatebirds foraging at sea flew in a continuous succession of climbs and descents, during both day and night, never remaining at the same altitude for a prolonged period (Fig. 2a). When climbing (average climbing rate, $0.40 \pm 0.14 \text{ m s}^{-1}$; maximum, 3.3 m s^{-1}), birds reached altitudes of up to 2,500 m (average maximum, $304 \pm 34 \text{ m}$); upper altitudes were similar during the day and at night. During descents (average rate, $0.38 \pm 0.15 \text{ m s}^{-1}$; maximum, 2.3 m s^{-1}), birds dropped to an average altitude of $89 \pm 23 \text{ m}$, rarely coming close to the sea surface (on average about once every $7.7 \pm 3.6 \text{ h}$), and then only during the daytime.

The birds' up-and-down flight pattern causes them to move slowly in a horizontal direction. Cross-country ground speeds were particularly low, averaging $10.0 \pm 0.8 \text{ km h}^{-1}$, and even lower at night ($8.6 \pm 2.0 \text{ km h}^{-1}$) than during the day ($11.3 \pm 1.7 \text{ km h}^{-1}$; paired *t*-test, $t=2.5$, d.f.=7, $P=0.036$). Birds covered an average of $223 \pm 208 \text{ km}$ per foraging trip (Fig. 2b), with a maximum range of 27–261 km.

Thermals are generally used by soaring birds by day over land⁵. Over tropical waters in regions affected by trade winds (which blow around the Equator from east to west), convection occurs under cumulus clouds to produce thermals⁶ that allow frigatebirds to soar continuously, day and night. Although the upward air movement in these thermals is slow³, the birds can soar effectively because of their reduced wing



Figure 1 A male magnificent frigatebird (*Fregata magnificens*) in flight off French Guiana. Note the exceptionally large wing area (wingspan, 2.4 m) and inflated gular pouch, which is used as a courtship signal. Frigatebirds spend almost all of their time in flight and are unable to settle on water because of their short legs and feet, and their inadequately waterproofed plumage.

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loading, allowing the costs of flight to be greatly reduced.

The constraint on frigatebirds to rely on thermals for flight may explain why these birds are restricted to trade-wind zones, where soaring conditions are optimal throughout the year³. We also tracked two birds during migration outside the breeding season and found that their flight speeds and movements were similar to those during the breeding period, indicating that these probably do not vary over the year.

We have shown that frigatebirds spend the night on the wing — like swifts⁷, the only other species known to do this. Our results also reveal that frigatebirds climb to unexpectedly high altitudes, where the temperature is much lower ($10\text{--}12 \text{ }^\circ\text{C}$ at 2,500 m) than at sea level ($27\text{--}30 \text{ }^\circ\text{C}$). Staying high in the air might be advantageous to frigatebirds, as it may allow them to search for the next thermal, as indicated by the presence of cumulus clouds or of climbing congeners, and to spot feeding opportunities on the sea surface.

Frigatebirds rely mostly on prey that is driven to the sea surface by underwater predators², which are mainly tuna; off French Guiana, estuarine dolphins (tuxuci) are often accompanied by large, multispecies bird flocks⁸ that can also probably be seen by these birds from long distances. Feeding opportunities are rare in these unproductive waters⁹, and our results confirm that frigatebirds only occasionally come close to the sea surface: feeding is presumably infrequent and occurs mainly during the daytime.

The scarcity of resources in tropical waters favours the survival of species whose flight proficiency enables them to travel slowly and economically⁹ between dispersed concentrations of prey. As a result, frigatebird provi-

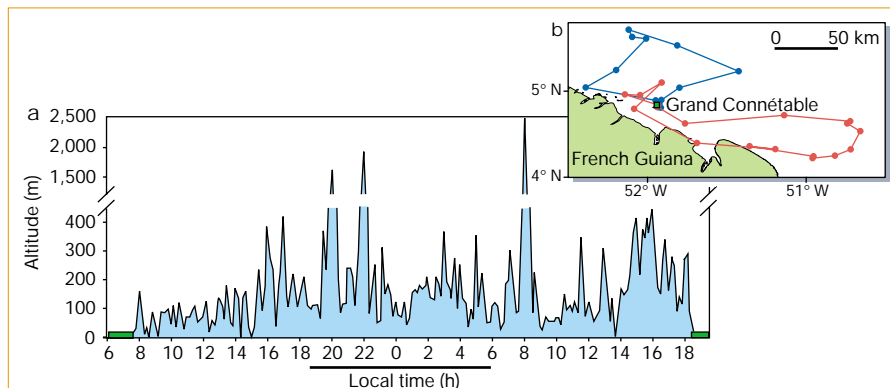


Figure 2 Foraging movements of flying frigatebirds, as revealed by altimetry (for vertical movements) and satellite telemetry (for horizontal movements). **a**, Vertical flight pattern of a sample female during a foraging trip, recorded over two days (24 and 25 April 2002). Black bar shows hours of darkness; green bars represent periods when the bird is in its nest in the colony. **b**, Horizontal movements of two frigatebirds (blue, brooding male; red, incubating female) foraging from the breeding colony (green box) and tracked by satellite telemetry.

sioning is low and their period of parental care is the longest of any bird². Their low reproductive rate and high life expectancy (more than 30 years) make them exceptional even among long-lived birds¹⁰ and, combined with their unusual morphology and foraging strategy, are examples of extreme adaptations to poorly provisioned tropical waters.

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1. Diamond, A. W. *Condor* **75**, 200–209 (1973).
2. Nelson, B. N. *Living Birds* **14**, 113–155 (1976).
3. Pennycook, C. J. *J. Exp. Biol.* **102**, 307–325 (1983).
4. Orta, J. in *Handbook of the Birds of the World Vol. 1* (eds del Hoyo, J., Elliott, A. & Sargatal, J.) 362–376 (Lynx, Barcelona, 1992).
5. Alerstam, T. *Bird Migration* (Cambridge Univ. Press, Cambridge, 1990).
6. Augstein, E. *Meteorology over the Tropical Oceans* (ed. Shaw, D. B.) (R. Meteorol. Soc., Bracknell, 1980).
7. Lack, D. *Swifts in a Tower* (Methuen, London, 1956).
8. Gould, P. J. in *Pelagic Studies of Seabirds in the Central and Eastern Pacific Ocean* (ed. King, W. B.) 6–52 (Smithsonian Inst., Washington, 1974).
9. Balance, L. T. & Pitman, R. L. *Proc. 22nd Int. Ornithol. Congr.* (eds Adams, N. J. & Slotow, R. H.) 2057–2071 (BirdLife S. Afr., Johannesburg, 1999).
10. Weimerskirch, H. in *Biology of Marine Birds* (eds Schreiber, E. A. & Burger, J.) 115–135 (CRC, Boca Raton, Florida, 2001).

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Pollinator attraction

Crab-spiders manipulate flower signals

Some European species of crab-spider match the colour of the flower on which they lie in wait to ambush insect pollinators, a tactic that is presumed to camouflage them from their intended prey and from predators^{1,2}. Here we show that the coloration of an Australian species of crab-spider, *Thomisus spectabilis*, which is cryptic on the white daisy *Chrysanthemum frutescens* to the human eye, is highly conspicuous to ultraviolet-sensitive insect prey — but that, instead of repelling foraging honeybees (*Apis mellifera*) as might be expected, the contrast of the spider against the petals makes the flowers more attractive. The spider is apparently exploiting the bee's pre-existing preference for flowers with colour patterning.

Visual signals communicated at ultraviolet wavelengths, which are invisible to humans and are therefore more difficult to analyse^{3,4}, may be used by ambush predators to manipulate their prey's behaviour and increase capture success. We have

investigated how *T. spectabilis* interferes with floral signals, and the effect of its visibility on the attractiveness of the flower to pollinating insects.

Under natural light conditions, we presented honeybees with pairs of randomly selected white daisies, one of which carried an anaesthetized spider, and recorded which of the two flowers the bee visited first. We then repeated the experiment using a plastic foil covering on each flower and spider; the cover blocked olfactory cues but was transparent to light of wavelengths greater than 300 nm.

Compared with empty flowers, the presence of white crab-spiders on the petals of daisies evidently attracted honeybees more, in both the presence and absence of olfactory cues (Fig. 1a). This indicates that the bees must have been guided by visual signals alone, and that the visual signal generated by the spider renders the flower more inviting to bees.

To identify this signal, we measured the spectral reflectance from 300 to 700 nm of the flower petals and of the spiders' abdomens. We calculated the colour contrast⁵ of the spiders against the flower petals and

computed the euclidean distances in the colour space of hymenopterans². We found that, compared with the flowers, white spiders reflect a considerable amount of ultraviolet light.

There was also a pronounced difference in the honeybee receptor-excitation values generated by spiders and flowers at ultraviolet wavelengths (Tukey-tests, $P < 0.001$ and $P < 0.001$, respectively), but not in the blue and green regions of the spectrum (ANOVA, $F_{2,74} = 136.8$, $P < 0.001$; Fig. 1b), where receptor excitation is comparable for both (Tukey test, $P = 0.901$). Consequently, instead of being cryptic, as they are to humans, the spiders produce a strong colour contrast that is detectable by their hymenopteran prey (mean euclidean distance in colour space \pm s.e., 0.14 ± 0.01 ; $n = 25$). The values for colour contrast are well above the detection threshold of 0.05 (ref. 2; one-sample *t*-test, $t_{24} = 7.6$, $P < 0.001$).

We conclude that *T. spectabilis* uses quite the opposite signalling strategy to that known to be used by other crab-spiders^{1,2}. *T. spectabilis* is difficult to perceive from far away, when bees use only their green-receptor signal to detect objects⁶, but is highly conspicuous in the insect visual spectrum when seen at close quarters. Because ultraviolet-reflecting white flowers are extremely rare in nature⁵, the spider will contrast strongly with almost any natural flower.

T. spectabilis will also be just as conspicuous to other flower visitors, as all known pollinating insects, including stingless bees⁷ (which are the spider's most likely Australian native prey), perceive ultraviolet light. We propose that the presence of spiders on flower petals creates a colour pattern that is particularly effective because bees have a pre-existing bias towards it — an idea that is consistent with empirical data showing that bees innately prefer flowers with strongly contrasting markings⁸.

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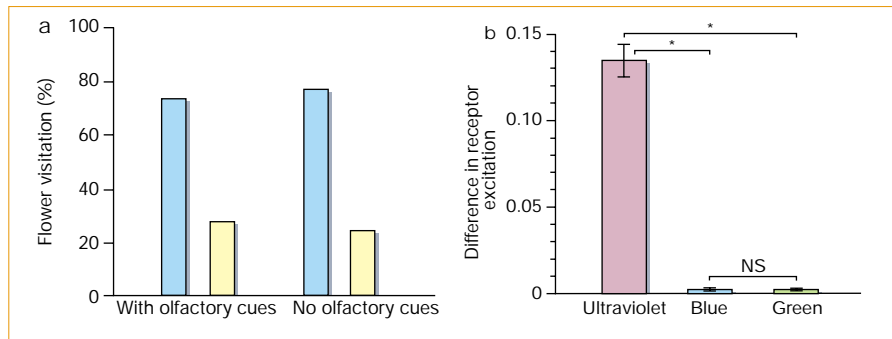


Figure 1 The effect of the presence of the crab-spider *Thomisus spectabilis* on the white daisy (*Chrysanthemum frutescens*) on flower visitation by honeybees (*Apis mellifera*). **a**, Proportion of bees that visit vacant daisies (yellow bars) and daisies occupied by spiders (blue bars) in the presence (binomial test, $n = 33$, $P = 0.0045$) and absence ($n = 25$, $P = 0.0053$) of olfactory cues. All spiders, flowers and bees were used only once. **b**, Difference in honeybee colour-receptor excitation values (mean \pm s.e.; for methods, see ref. 2) between spiders' abdomens and daisy petals at different wavelengths (ultraviolet receptors, $\lambda_{\text{max}} = 345$ nm; blue receptors, $\lambda_{\text{max}} = 440$ nm; green receptors, $\lambda_{\text{max}} = 535$ nm; ref. 7). Tukey test, asterisk denotes $P < 0.001$; NS, not significant.

1. Chittka, L. *Entomol. Genet.* **25**, 181–187 (2001).
2. Thery, M. & Casas, J. *Nature* **415**, 133 (2002).
3. Endler, J. A. *Biol. J. Linn. Soc.* **41**, 315–352 (1990).
4. Bennett, A. T. D., Cuthill, I. C., Partridge, J. C. & Lunau, K. *Proc. Natl Acad. Sci. USA* **94**, 8618–8621 (1997).
5. Chittka, L., Shmida, A., Troje, N. & Menzel, R. *Vision Res.* **34**, 1489–1508 (1994).
6. Giurfa, M., Vorobyev, M., Brandt, R., Posner, B. & Menzel, R. *J. Comp. Physiol. A* **180**, 235–243 (1997).
7. Briscoe, A. D. & Chittka, L. *Annu. Rev. Entomol.* **46**, 471–510 (2001).
8. Lunau, K., Wacht, S. & Chittka, L. *J. Comp. Physiol. A* **178**, 477–489 (1996).

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