Are hand-raised flying-foxes (*Pteropus conspicillatus*) better learners than wild-raised ones in an operant conditioning situation?

Brigitta Flick[1], Hugh Spencer[2] and Rick van der Zwan[3]

[1] James Cook University, Department of Psychology, Cairns Qld, Australia
brigitta.flick@jcu.edu.au
[2] Australian Tropical Research Station, PMB 5 Cape Tribulation via Mossman Qld, Australia
hugh@austrop.org.au
[3] Southern Cross University, School of Psychology, Coffs Harbour NSW, Australia
rick.vanderzwan@scu.edu.au

ABSTRACT

This study was undertaken to gain some knowledge of Flying-fox (Megachiroptera: Pteropodidae) learning ability, using 10 Spectacled Flying-foxes *Pteropus conspicillatus* in a free-operant conditioning paradigm. The subjects were trained to pull levers for a juice reward in the controlled environment of a modified Skinner box. All sessions were monitored and recorded on video. During the course of the experiment a difference was found in the learning behaviour between the three hand-raised and the seven wild-raised subjects. The three hand-raised Flying-foxes learned the task in the seventh, ninth or fourteenth 10-minute session whereas the wild-raised animals did not learn to pull the levers. When returned to the experimental chamber more than three years later two of the hand-reared subjects immediately pulled the levers to receive juice. It showed that these animals remembered the experimental chamber, the location and the reward for pulling the levers.

Key words: *Pteropus*, Flying-fox, behaviour, learning, operant conditioning, enriched environments

Introduction

Flying-foxes (sub-order Megachiroptera) can be quite large, up to 1.5 kg, are vegetarian and live mostly in the open canopies of trees (Neuweiler 2000; Churchill 1998). They possess no sonar but have good vision, especially at low light levels (Neuweiler 1962). The large fruit bats of the genus *Pteropus* are represented by four species in Australia. They inhabit the forests along the North and East Coast from Broome through Cape York Peninsula to Melbourne (Williams *et al.* 2006; Churchill 1998; Strahan 1995). The Spectacled Flying-fox *Pteropus conspicillatus*, the subject in this study, is restricted to the rainforests of the tropical north of Queensland, Australia.

The Spectacled Flying-fox appears in all known biological and physiological ways virtually identical to the other two large *Pteropus* species in Australia, the Grey-headed Flying-fox *Pteropus poliocephalus* and the Black Flying-fox *Pteropus alecto* (Martin *et al.* 1996; McIlwee and Martin 2002). While the three species are restricted to certain areas of the Australian continent, they overlap in their ranges and retain the capacity to interbreed (Martin *et al.* 1996). Flying-foxes are considered an integral part of the Australian forest and have long been recognised as important pollinators in the eastern coastal forests of the continent especially of the Australian hardwood (Eucalypt) timber (Eby 1991; Richards 1990b; Nelson 1965b; Ratcliffe 1947). The population of the Spectacled Flying-fox has been reduced, as coastal forests and roosting sites have been destroyed (Garnett *et al.* 1999; Richards 1990a) and because of this loss of natural habitat the animals have moved into areas where their presence impacts on human activities (Martin and McIlwee 2002; Williams *et al.* 2006; Van der Ree *et al.* 2006). As a consequence of their move into urban and farming areas, human impact on both the Spectacled and the Grey-headed Flying-fox has called the survival of these species into question (McIlwee and Martin 2002). This led to their inclusion into the list of vulnerable species compiled in accordance with the Environmental Protection and Biodiversity Conservation Act of 1999 (EPBC Act, Environment Australia 2002). The conservation of the Flying-foxes is urgent and any insight into their behaviour could assist in the development of management strategies in Australia.

Flying-fox diurnal behaviour in the wild has been studied and extensive observations reported on territoriality, courtship, mother-infant interactions and vocal communications (Christesen and Nelson 2002; Markus 2002; Markus and Blackshaw 2002), social organization, social behaviour, and modes of locomotion (Nelson 1965b).Their behaviour at night is more difficult to observe since the animals leave their day roosts and can feed up to 30 km away. They are also known to cover vast areas in seasonal movements (Churchill 1998; Spencer *et al.* 1991; Eby 1991; Nelson 1965; Richards 1990a, b). Radio-tracking studies and observations (Spencer *et al.* 1991; Eby 1991; Nelson 1965a; Richards 1990a, b) indicate that Flying-foxes make use of long-term and visual memory: they cover thousands of square kilometres annually in their search for food and for traditionally used colony sites. They have often been observed "trap-lining", i.e. visiting areas known in the past to be a productive resource, as if to "check" on progress of flowering and fruit ripening (H. Spencer, pers. obs. 2003, ATRS).

Pp. 86–91 in *The Biology and Conservation of Australasian Bats*, edited by Bradley Law, Peggy Eby, Daniel Lunney and Lindy Lumsden. Royal Zoological Society of NSW, Mosman, NSW, Australia. 2011.

Flying-fox learning behaviour *per se* has not been studied in the wild and only one study has reported on their learning in the laboratory. Indian Flying-foxes *Pteropus giganteus* were trained in a forced choice procedure to investigate their visual acuity and the limits of brightness perception (Neuweiler 1962).

Operant conditioning

Flying-foxes in the wild pull branches with flowers or fruit towards them with their elongated thumb claw to lick or bite them. This natural behaviour seems to lend itself to being adapted to learning a lever-pulling task in an operant conditioning paradigm if, as the data reported by Neuweiler (1962) suggest, the capacity for instrumental learning is general among Flying-foxes. With that in mind the original aim of this study was to observe the learning behaviour and capability of Spectacled Flying-foxes in a free operant conditioning procedure with the view of establishing a useable conditioning procedure for the investigation of visual and olfactory abilities. During training for that study differences between the behaviours of hand-reared and wild Flying-foxes became apparent and those learning differences are the focus of the data here reported.

Methods

Subjects

Ten Spectacled Flying-foxes: seven males and three females, ranging in ages from 3 to an estimated 15 years, were selected for this study. All of them were permanent captive animals held at the Cape Tribulation Tropical Research Station (subjects 1 to 5) or at the "Batreach" Rescue and Rehabilitation Centre in Kuranda (subjects 6 to 10).

Subjects 4 (male), 5 (female) and 9 (female) were the only participants of whom the ages were accurately known, 10, 9 and 3 years, respectively. All three had been hand-raised from the age of between one and four weeks. All other subjects were rescued as adult or older juvenile wild animals and rehabilitated, but had been judged to be incapable of surviving in the wild, either because of wing injury and/or because they had been kept as pets for over a year, and therefore could not be released. These animals had been in captivity for between 3 and 10 years. Flying-foxes need to learn foraging and other skills from the group during their approximately 2–3 year period before full sexual maturity (Churchill 1998). All the Flying-foxes were tame and familiar with the experimenter.

Selection of Subjects

Subjects were selected for inclusion into this study according to a set suitability criteria: Physical well-being, having two functional thumb claws, and general behavioural suitability. Of the five animals selected from the group at Cape Tribulation, subjects 4 and 5 completed the study described here. Subjects 1, 2 and 3 were selected for training, but eventually were discontinued because they failed to learn the training task. Those three Flying-foxes showed a lack of inquisitiveness and occasionally behaved in an agitated and stressed manner when put in the test chamber. Of the five subjects at "BatReach" in Kuranda, four exhibited occasional inquisitive behaviour and occasional lever pulling, but training was discontinued after between 17 and 35 training sessions when it became clear that they were never to learn the task. Only one, subject 9, showed the required learning ability.

Apparatus

The experimental chamber was trapezoidal in cross section (470 mm by 970 mm wide, 970 mm high, 470 mm deep, Figure 1).

The sidewalls and the two front doors had wooden frames lined inside with Corflute panels. The ceiling and the floor were made of wood panels. A perch hung from the ceiling was adjustable in length to accommodate the size of the Flying-fox subject.

The two response levers were mounted on the back panel of the experimental chamber. The juice reservoir and part of the control circuitry were on the back of the wooden panel. The blue feeder cup consisted of a 2ml plastic measuring spoon mounted on a wooden support protruding 200 mm from the panel, which was positioned to be easily reached by the Flying-fox hanging on the perch. The cup was wide enough to accommodate the Flying-fox's snout and shallow enough to allow the animal's tongue to reach the bottom. The fruit juice (mango or apricot nectar were equally eagerly accepted by all subjects) was delivered via a plastic tube through a hole in the cup in 0.3 ml aliquots.

A solenoid valve activated by an external controller box delivered juice from the reservoir to the cup. A buzzer also sounded every time the solenoid was activated serving as an auditory clue to indicate that the lever had been pulled properly.

The response levers consisted of 20 cm long, 1 mm diameter flexible stainless steel wires, which fitted into a tube, soldered onto a micro-switch lever and set to respond to a pull of about 50 g at an angle of 30 degrees. The micro-switches were connected to the controller box which activated the buzzer and the juice reward solenoid.

The levers were fitted with a plastic ring (30 mm diameter) at the end to attract the attention of the subject and make it easy for the bat to hook them. Other items such as a yellow ball and small plastic ornaments were also tried with the non-inquisitive subjects in an attempt to attract their attention.

A small black and white television camera was mounted in the ceiling of the box so that the animal's responses could be seen when the chamber was closed and the picture and sound recorded for later analysis. A small desk lamp mounted above the box gave adequate illumination ($0.3 cd/m^2$) inside the box.

The experimental chamber was demountable and was used in both locations.

Procedure

Preliminary training. Each subject was taken out of the communal cage and carried to the experimental chamber, positioned on the perch and left to look around for a few minutes to familiarise itself with the surroundings. The delivery cup contained some juice as an incentive to investigate the apparatus. The shaping sessions were then started by closing the box doors and observing the action on the television screen.

Training. Lever-pull responses were shaped by rewarding successive approximations of the desired response.

The animals had water withheld for 8 hrs prior to testing.

Acquisition, extinction and re-acquisition. During the acquisition sessions of 10 min duration, each clear deliberate lever pull by the Flying-fox was rewarded with juice. This acquisition phase was considered complete when the rate of lever pulls stayed constant or the subject seemed to be sated during the sessions. In the extinction sessions of 10 min duration no reward of juice was given no matter how often the levers were pulled. The extinction sessions started 4 hours after the last acquisition session for subjects 4 and 5, and 1 day for subject 9. The re-acquisition sessions commenced two days after the last extinction session. The re-acquisition sessions were identical to the acquisition sessions in that the subject was given a juice reward when the levers were pulled.

Results

The learning performance of the Flying-foxes was measured in number of lever pulls per 10 min session. Three Flying-foxes learned the task in the seventh, ninth or fourteenth 10-min session. The lever pull responses of these three Flying-foxes during acquisition, extinction and re-acquisition sessions of 10 min are plotted in Figure 2. Only the last six acquisition sessions before the extinction phase are shown.

Memory. Three and a half years after the conclusion of the study three of the original participating Flying-foxes at the Cape Tribulation Tropical Research Station were put back into the chamber. The original non-learner (Subject 3) only licked the cup dry and then looked around (Figure 3). Subjects 4 and 5 who originally had learned the lever-pulling behaviour demonstrated persistence of learning by pulling the levers after licking the cup dry, and did so without any hesitation. The photo strip in Figure 4 shows the behaviours of Subject 4. The third learner (Subject 9) was not available for testing because the Flying-fox still lived at the "Batreach" Rescue and Rehabilitation Centre in Kuranda.

Discussion

The aim of this study was to investigate the learning of Spectacled Flying- foxes in a free operant conditioning task using an experimental chamber. Only three subjects out of ten subjects learned the task. These were the only hand-raised animals in the group. They were of different ages and had not been reared by the same carer or at the same site. Their only common link is their early life environment as they spent it in the care of humans from the age of 3 to 4 weeks. The wild-raised animals had come to the rehabilitation centres as wild adults or older juveniles and could not be released for various reasons. These Flying-foxes were nevertheless used to humans and were tame enough to handle. On retesting after 3.5 years the hand-raised Flying-foxes showed persistence in learning when they immediately performed the task of pulling the levers to receive a juice reward, while the animals that had never learned the behaviour did not show any change.

The training of wild Flying-foxes to find food using a discrimination task has been reported by Neuweiler (1962). The difference between Neuweiler's studies and the present one is that in the present study, no food

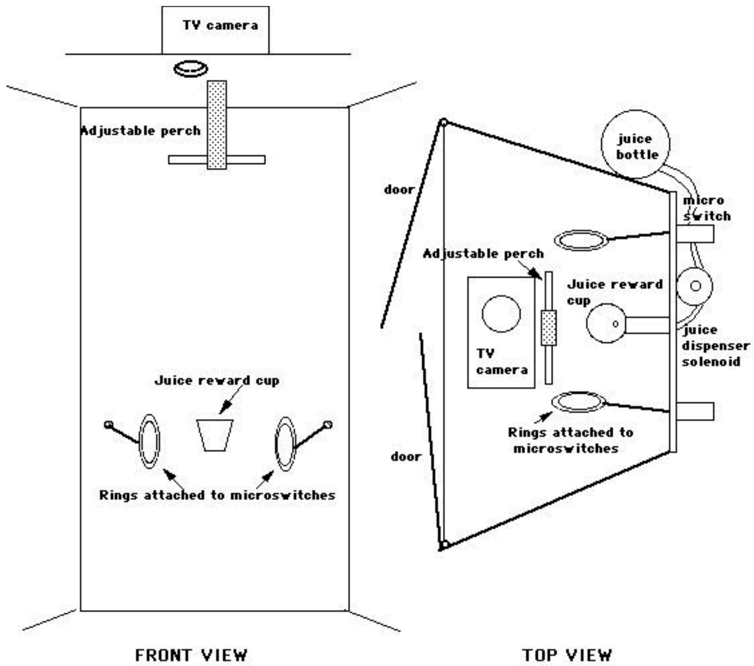

Figure 1. Front view of the experimental chamber showing the dimensions, and the position of the response levers and the feeding cup. The position of the hanging perch suspended from the ceiling is indicated. Not shown are the two side panels and the top and bottom panels, which create the 'box' itself. The entire enclosure is fitted with 2 doors that can be closed to visually isolate the animal from the surroundings.

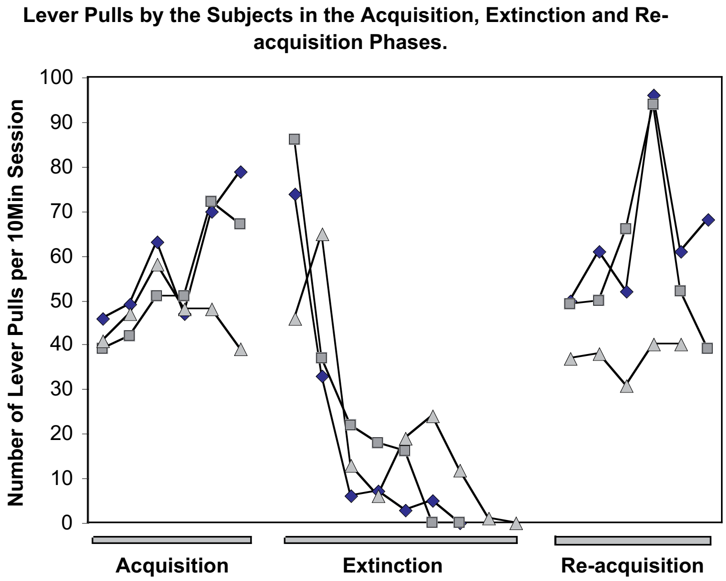

Figure 2. Pattern of lever pull responses per 10 min sessions during acquisition, extinction and re-acquisition for subject 4 (diamond), subject 5 (square) and subject 9 (triangle).

Figure 3. Subject 3 was unable to interact with the conditioning process 3.5 years ago, and he behaves in exactly the same fashion as before.

Figure 4. Subject 4 is immediately pulling the levers and drinking juice from the central blue cup 3.5 years after having learned the conditioned behaviour described in this paper. The yellow balls fitted to the lever wires are quite evident in this photograph.

deprivation was used, only a very mild fluid deprivation. It should be pointed out that in the wild, these Flying-foxes seldom drink, satisfying their water requirements with food; so, a 12 hour water deprivation would not have constituted a major drive.

The failure of wild-raised Flying-foxes to learn the lever pulling response seems to indicate that the rearing history of the animals represents the major difference. When observing the animals in the communal cage no distinctive behaviour could be detected separating the hand-raised from the wild-raised.

Individual differences itself could not have been the decisive factor since the three learners displayed different displacement activities in later extinction sessions ranging from being active and clambering around in the experimental chamber (subjects 4 and 5) to resting for almost the entire session (subject 9). Allowing for individual differences, the results of the study indicate that the actual manipulation component of the task was the stumbling block for the wild-raised animals.

In the light of the suggested close phylogenetic relationship of Flying-foxes with prosimians (Pettigrew 2000), this possibility is substantiated by studies with six different lemur species where the animals paid minimal attention to "gadgets" (Jolly 1964a and b; 1966). The researcher concluded that these (non hand-reared) animals did not exploit their capacity for inquisitiveness toward non-food objects, instead their learning was concentrated on fast acquisition of the social structure, especially on the social status of the group members as well as their own and that behaviours are learned in the social environment by imitation rather than by individual discovery. Thus the capability for operant learning may be limited after maturity is reached. In the case of the hand-reared Flying-foxes this capability would have been preserved or carried over as an adult behaviour.

The developmental stages of lemurs from birth to breeding are comparatively long and similar to Flying-foxes. Gestation time is three to five months, depending on the species, maturity is reached at 18 months, and breeding age at two years. The long relationship with the mother facilitates an imitative learning style. The large Flying-foxes (*P. conspicillatus*) used in this study have a similar early life pattern. They are born after six months gestation and depend on the mother for milk for up to six months (Martin *et al.* 1996, Nelson 1965) Maturity is also reached at two years of age and Flying-foxes live in a similar interactive social environment to that of lemurs.

Another explanation could be sought in the unnatural situation of staying in the same spot and pulling the same two levers toward them, which for a wild animal is unnatural (keeping in mind the supposition that the window of learning to investigate gadgets has closed in these adults). This could be explained according to Seligman's principles in conditioning (1970) as 'contra-preparedness' and therefore inability to learn. In our experimental situation the wild raised Flying-foxes might be contra-prepared to pull and lick, because the set of behaviours that they have learned some time in their early life which enables them to feed on nectar in flowering trees includes moving about and pulling branches from different directions. However, Flying-foxes that were hand-reared never had to acquire a set way of feeding and in a 'gadget enriched' environment they most likely developed additional behavioural and conceptual skills (preparedness) that wild animals do not have. Seligman's categories of learning ability should be considered in future learning studies with Flying-foxes.

The study suggests that within the same species, the learning capability can vary according to the animal's history of familiarity with the 'artificial' environment in early life. In the hand-raised animals a greater plasticity of behaviour may be preserved into adulthood, mimicking a juvenile state. Personal experience and anecdotal reports from Flying-fox carers attest to the curiosity and exploratory behaviours these hand-raised animals retain till late in their life. It should also be noted that Flying-foxes in the wild have to learn as young juveniles how to find food and to integrate into the ever-changing social hierarchy of a wild colony. In contrast, hand-reared animals in human care are provided with food and are part of a more or less stable social environment in the cage. Therefore, they do have leisure to explore their environment and might develop more fully a capacity to interact with artefacts at a critical stage in their life.

The knowledge gained of the Flying-foxes' behavioural psychology could be a start in understanding the animals' perceptual abilities that enable them, for instance, to navigate over large areas, remember the location of seasonal food and roosting sites, often over areas of thousands of square kilometres, and to convey this knowledge to their offspring. Obtaining and applying this knowledge in practical ways could mean that the conservation as well as the management of these animals will benefit. A controlled study replicating the results from this paper with a larger number of subjects would be necessary to elucidate differences in learning capabilities of hand-reared and wild-reared Flying-foxes and to test the question of the existence of a "window of learning by exploration". It would have to consist of Flying-foxes which have been reared in strictly different environments. One group would be hand-reared in a gadget-enriched environment from an early age (1 to 2 weeks) and another would be reared by their mothers in a communal cage with other Flying- foxes. Such conditions could be readily created for example with animals from the tick rescue program at the Tolga Bat Hospital. The need to keep unreleasable Flying- foxes for research purposes is very real and the policy of killing such animals should be reviewed.

Acknowledgements

Special thanks to Pam Tully, Anabelle Olssen, the volunteers at the Cape Tribulation Tropical Research Station, and photographer Bruce Allen. We also thank two anonymous reviewers for their comments. The research was carried out under EPA permit WISP01287603. The construction of the experimental chamber was made possible through the assistance of the Australian Tropical Research Foundation.

References

Christesen, and Nelson 2000. Vocal communication in the grey-headed flying fox. *Australian Zoologist* 31: 447–457.

Churchill, S. 1998. *Australian Bats.* New Holland Publishers, Sydney.

Dragoi, V., and Staddon, J.E.R. 1999. The dynamics of operant conditioning. *Psychological Review* **106**: 20–61.

Eby, P. 1991. Seasonal movements of grey-headed flying foxes, *Pteropus Poliocephalus* (Chiroptera: Pteropodidae), from two maternity camps in northern New South Wales. *Wildlife Research* **18**: 547–560.

Garnet, S., Whybird, O. and Spencer, H. 1999. The conservation status of the spectacled Flying fox *Pteropus conspicillatus* in Australia. *Australian Zoologist* **31**: 198–207.

Jolly, A. 1964a. Prosimians' manipulation of simple object problems. *Animal Behaviour 12*: 560–570.

Jolly, A. 1964b. Choice of cue in prosimians learning. *Animal Behaviour 12*: 571–577.

Jolly, A. 1966. Lemur social behaviour and primate intelligence. *Science* **153**: 501–506.

Markus, N. 2002. Behaviour of black flying fox, *Pteropus alecto*: 2. Territoriality and courtship. *Acta Chiropterologica* 4 (2): 153–166.

Markus, N. and Blackshaw, J.K. 2002. Behaviour of the black flying fox, *Pteropus alecto*: 1. An ethnogram of behaviour, and preliminary characterisation of mother-infant interactions. *Acta Chiropterologica* 4 (2): 137–152.

Martin, L. and McIlwee, A.P. 2002. The reproductive biology and intrinsic capacity for increase of the grey-headed flying fox *Pteropus poliocephalus (*megachiroptera), and the implications of culling. Pg. 91–108 in Managing the Grey-headed Flying-fox as a Threatenend Species in New South Wales, edited by P. Eby and D. Lunney. Royal Zoological Society of New South Wales, Mosman, NSW.

Mazur, J.E. 1994. *Learning and Behaviour* (third edition). Prentice Hall, Englewood Cliffs, New Jersey.

McIlwee, A.P. and Martin, L. 2002. On the intrinsic capacity for increase of Australian flying-foxes (*Pteropus* spp., Megachiroptera). *Australian Zoologist* **32**: 76–100.

Nelson, J.E. 1965a. Movements of Australian flying foxes (Pteropodidae: Megachiroptera). *Australian Journal of Zoology* **13**: 53–73.

Nelson, J.E. 1965b. Behaviour of Australian Pteropodidae (*Megachiroptera*). *Animal Behaviour* **13**: 544–557.

Neuweiler, G. 1962. Bau und Leistung des Flughundauges. *Zeitschrift der vergleichenden Physiologie* **46**:13–56.

Neuweiler, G. 2000. *The Biology of Bats.* Oxford University Press, New York.

Pettigrew, J. 2000. http://www.uq.edu.au/nuq/jack/consensus.htm

Ratcliffe, F. 1947. *Flying Fox and drifting Sand.* Angus and Robertson, Sydney.

Richards, G.C. 1990a. The spectacled flying-fox, *Pteropus conspicillatus* (Chiroptera:Pteropodidae), in north Queensland 1. Roost sites and distribution patterns. *Australian Mammalogy* **13**:17–24.

Richards, G.C. 1990b.The spectacled flying-fox, *Pteropus conspicillatus* (Chiroptera: Pteropodidae), in north Queensland 2. Diet, seed dispersal and feeding ecology. *Australian Mammalogy* **13**: 25–42.

Richards, G.C. and Spencer, H.J. 1995. *Pteropus conspicillatus*. Pp. 435–437 in The Mammals of Australia, edited by R. Strahan. Reed Books, Chatswood, NSW.

Seligman, M. 1970. On the generality of the laws of learning. *Psychological Review* **77**: 406–418.

Spencer, H.J., Palmer, C., and Parry-Jones, K. 1991. Movement of fruit-bats in eastern Australia, determined by using radio-tracking. *Wildlife Research* **18**: 463–468.

Strahan, R. (ed.) 1995. *The Mammals of Australia.* Sydney. Reed Books, Chatswood, NSW.

Williams, N.S.G., McDonnell, M.J., Phelan, G.K., Keim, L.D., and Van der Ree, R. 2006. Range expansion due to urbanization: Increased food resources attract Grey-headed Flying-foxes (*Pteropus* ***poliocephalus***) to **Melbourne.** *Austral. Ecology* **31**: 190–198.

Van der Ree, R., McDonnell, M.J., Tempy, I., Nelson, J, and Whittingham, E. 2006. The establishment and dynamics of a recently established urban camp of flying foxes (*Pteropus* ***poliocephalus)*** outside their geographic range. *Journal of Zoology (London)* **268**: 177–185.

Wynne, C.D.L. 2001. *Animal cognition. The mental lives of animals,* Palgrave, New York.