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Albatross Long-Distance Navigation: Comparing Adults And Juveniles

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This paper was first presented at RIN 05, the 5th quadrennial conference on Orientation and Navigation in Birds, Humans and other Animals which was held at the University of Reading between 6–8th April 2005.

Albatrosses are known for their extreme navigation performance enabling them to locate isolated breeding islands after long-distance migrations across open seas. Little is known about the migration of young albatrosses and how they reach the adults' navigation and foraging skills during the period of immaturity lasting several years and spent permanently flying across the open ocean. We tracked by satellite telemetry the dispersal and migration of 13 juvenile wandering albatrosses from the Crozet Islands during their first year at sea. The young albatrosses covered an average distance of 184,000 km during the first year, restricting their dispersal movement to the unproductive and low wind subtropical Indian Ocean and Tasman Sea. The juveniles initiated the migration by an innate phase of rapid dispersal encoded as a fixed flight direction assisted by southerly winds towards north and northeast. Thereafter each individual restricted its movement to a particular zone of the ocean that will possibly be used until they start breeding 7–10 years later and return in contact with breeding adults. This dispersal in young birds corresponds well with movements observed for adult non-breeding wandering albatrosses. The results show clearly an inherited ability to navigate back to already visited areas in young wandering albatrosses. The juvenile dispersal behaviour and migration at sea suggest a genetically based migration program, encoding navigation to a destination area used throughout the life.

KEY WORDS

- 1. Migration. 2. Wandering albatrosses. 3. Diomedea exulans. 4. Bird navigation.
- 1. INTRODUCTION. Albatrosses are known for their impressive navigational abilities enabling them to successfully locate isolated breeding islands and to cover thousands of kilometres during migrations across open seas (e.g. Warham 1990). Despite these impressive navigational performances, it is still largely unknown which cues they use for navigation and how they are able to locate these remote sites (e.g. Papi and Luschi 1996, Åkesson 1996, 2003, Åkesson and Alerstam 1998, Bonadonna et al. 2003a).

Migrating animals can use a number of different strategies to navigate over large geographical areas, based on ego- or geo-centric information (e.g. Wallraff 1990, Papi

1992, Dusenbery 1992, Wiltschko and Wiltschko 1995, Lohmann and Lohmann 1996a, Wehner 1998, Luschi et al. 2001, Able 2001, Åkesson 2003, Åkesson et al. 2003). For instance, recent experiments with loggerhead turtles Caretta caretta migrating in the Atlantic Ocean show that the hatchlings rely on an inherited program, in which they use a number of different cues to find their way to open ocean (Lohmann and Lohmann 1996b, 1998). The program is encoded as a sequence of behavioural responses that is triggered first by visual cues on the beach, then wave direction as the hatchlings enter the sea and later in the open ocean they are guided by geomagnetic cues (Lohmann and Lohmann 1994, 1996a and b, 1998). Loggerhead hatchlings respond to artificial magnetic fields by changing their preferred courses recorded in circular test arenas, when exposed to artificial magnetic fields simulating local combinations of total field intensity and angles of inclination (Lohmann et al. 2001), suggesting an ability to navigate by using geomagnetic information. Both total field intensity and inclination angle vary over the Earth's surface (Skiles 1985) and can, in theory, be used in many areas to locate geographical sites (Lohmann and Lohmann 1996a, Åkesson 1996, Phillips 1996, Walker 1998); this has been supported by simulated magnetic displacements (e.g. Fischer et al. 2001, Lohmann et al. 2001, Boles and Lohmann 2003, cf. Papi et al 2000). However, due to the secular variation of the geomagnetic parameters and alignment of geomagnetic gradients this possibility might be limited in some geographical areas (e.g. Lednor 1982, Courtillot et al. 1997, Åkesson and Alerstam 1998, Wallraff 1999). The South Indian Ocean around the Crozet Island Archipelago, as opposed to the South Atlantic Ocean, is one of these areas where magnetic bi-coordinate navigation seems to be complicated (Åkesson and Alerstam 1998), and it is not known whether animals use a bi-coordinate geomagnetic map to navigate in this area.

Experiments with procellariiform seabirds have shown that odours are important for locating food at sea (e.g. Grubb 1972, Lequette et al. 1989, Nevitt et al. 1995), locating specific nest sites on isolated islands (e.g. Bonadonna and Bretagnolle 2002, Bonadonna et al. 2003a and b) and partner recognition (Bonadonna and Nevitt 2004). Dimethyl sulphide emitted by phytoplankton is the source of information guiding procellariiform seabirds like petrels, prions and shearwaters, to rich food patches at up-welling zones at continental shelf areas etc, and which can be very local in the marine environment (e.g. Nevitt et al. 1995, Nevitt 2000). However, albatrosses do not seem to use this source of information (Nevitt et al. 1995) or odours emitted from cod liver oil and krill (Lequette et al. 1989, Nevitt 1999) to the same extent as other procellariiform bird species, and thus, it is unclear to what extent albatrosses rely on odours for navigation in their marine environment as well as for locating their breeding sites (e.g. Bonadonna and Bretagnolle 2002, Bonadonna et al. 2001, 2003a). Furthermore, it is unknown what cues are used during the first migration and how the navigation system develops in juvenile albatrosses during the first years at sea.

We used satellite telemetry (Argos) to track the first year dispersal and migration in juvenile wandering albatrosses breeding at the Crozet Islands in the south Indian Ocean. We were interested to investigate in which areas of the ocean the adult and juvenile birds spent the nonbreeding period compared to the foraging zone used during breeding (i.e. adults) and by which routes the birds reached these areas. We compared the routes selected by juvenile wandering albatrosses with those recorded for adult non-breeding birds leaving the breeding island after a breeding attempt

(Weimerskirch and Wilson 2000). We were interested to find out if the movement patterns would reveal whether the young albatrosses rely on a simple genetic program encoding distance and direction to reach the migration goal (e.g. Berthold 1996), or if their movements indicated inherited navigation skills, enabling them to return to local geographical areas at sea. We also estimated the distances covered during the first year of migration in juvenile birds and recorded the daily distances covered for juvenile compared to adult wandering albatrosses. The movements of juvenile birds were compared with tracks of non-breeding adults from the same breeding sites.

- 2. MATERIAL AND METHODS. To record the movements of juvenile wandering albatrosses we attached satellite transmitters (Microwave PTT 100) to 13 (6 males and 7 females) fully feathered juvenile individual birds in mid-November 2001 (7 individuals) and 2002 (6) at the Crozet Islands, south-western Indian Ocean (Weimerskirch et al. submitted). We used six solar panel powered 35–50 g satellite transmitters with a duty cycle of 10 h on and 24 h off, and seven 35-45 g battery powered satellite transmitters with a duty cycle of 10-18 h on and 54 h off fitted with adhesive tape on the back feathers. The locations of transmitters were determined using the Argos system (http://www.argosinc.com/), normally resulting in between 4 and 14 uplinks per day. All locations obtained (all classes) were filtered following Weimerskirch et al. (1993) removing locations which necessitated a speed of travel of >90 km/h, and locations that were obtained at less than 10 minute intervals. Total distance covered during the year was estimated from the distance covered during periods of transmission, and taking into account the proportion of time when the transmitter was on duty cycle OFF (Weimerskirch et al. submitted). We compared the movements of juvenile wandering albatrosses with those recorded by light intensity loggers for adult birds breeding at the same sites and tracked during the non-breeding period (Weimerskirch and Wilson 2000).
- 3. RESULTS. The migration movements of 13 juvenile wandering albatrosses were tracked for between 2 and 13 months (average 5.6 months). Three satellite transmitters stopped transmitting prematurely, after 66, 69 and 83 days, possibly because the birds died. All juveniles showed similar dispersal behaviour, during which time they left the breeding island without assistance from their parents. First after leaving the island the juveniles immediately landed on water, and drifted off the birthplace for 1–15 days, they waited for assistance from southerly winds before initiating a rapid directional movement to the north-north-east, until they crossed the subtropical convergence 600 km to the north of the Crozet Islands (Weimerskirch et al. submitted). Thereafter they started a continuous movement in the sub-tropical waters, which differed in destination area used between individuals (three examples of tracks lasting 112, 157 and 266 days and covering 16974, 44785 and 62318 km, respectively, are presented in Figure 1).

The movement patterns and especially the departure behaviour were strongly influenced by wind direction. Changes in flight direction were always associated with changes in wind direction, but during this time all juvenile albatrosses remained strictly north of the subtropical convergence in the Indian Ocean and Tasman Sea.

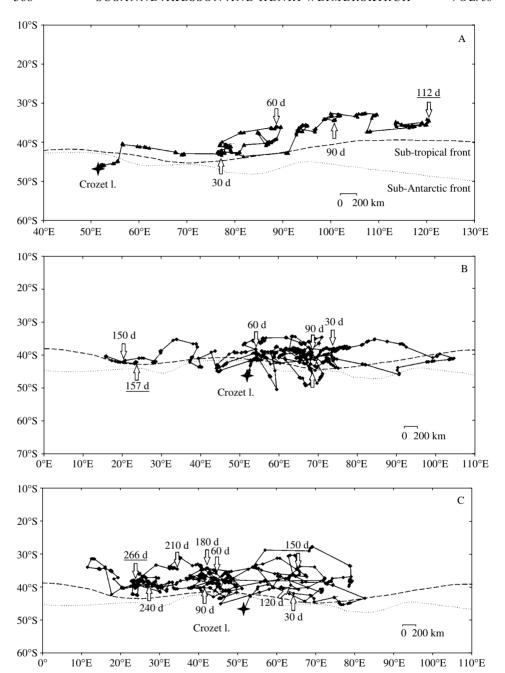


Figure 1. Satellite tracks of three young wandering albatrosses (A: 1391, B: 8959a, C: 25751) migrating from Crozet Islands in 10 December, 22 and 30 November 2001, respectively. Time intervals in 30 days after departure and total time (underlined) are indicated for each track. The starting point located at the Crozet Island is indicated by a star and the Sub-tropical and Sub-Antarctic fronts are indicated by broken and dotted lines, respectively.

The overall dispersal zone of the Crozet Island juvenile wandering albatrosses overlaps little with the foraging zones of breeding adults from the major breeding sites (Weimerskirch et al. submitted). After six months birds restricted their range to a more specific sector, generally south of Australia (see Figure 2c). During the first year of life the estimated average distance covered by a juvenile wandering albatross was $183,800 \pm 34,100$ km (range 127,020-267,000 km; Weimerskirch et al. submitted), corresponding to a distance of 4-6 times around the Earth. The tracks of adults demonstrate similar movement patterns as used by the juvenile birds (Weimerskirch and Wilson 2000), but with more direct routes to the non-breeding destination areas, suggesting the adults were heading for areas revisited before (Figure 2).

4. DISCUSSION. Despite the extreme wide-ranging capacities of wandering albatrosses (Weimerskirch and Wilson 2000), our satellite trackings of juveniles born at Crozet Islands show that they restricted their dispersal to one ocean basin, the southern Indian Ocean and Tasman Sea (Weimerskirch et al. submitted). These movement patterns are very similar to what adults show during their sabbatical year when they are no more constrained by central place foraging in the vicinity of the breeding island (Weimerskirch and Wilson 2000). During the non-breeding period adult wandering albatrosses also remain in specific sectors that are restricted to the Indian Ocean and Tasman Sea (Weimerskirch et al. 1985, Weimerskirch and Wilson 2000). However, several individuals moved frequently back and forth across longitudes (east-west), but remained within the same latitudinal sector of the ocean (Figure 1). The foraging zones of juveniles were different from those of breeding adults and are restricted to the subtropical part of Indian Ocean, a zone that is overall much less productive than the sub-Antarctic waters favoured by adults (Weimerskirch et al. submitted).

As many passerines, juvenile albatrosses migrate on their own and thus the migration is most likely the result of an innate genetic program possibly in combination with acquired navigational skills (for reviews, e.g. Clobert et al. 2001, Dingle 1996, Berthold 1996, Alerstam et al. 2003). Their ability to migrate from and return strictly to their birthplace after years of immaturity in the open ocean (Inchausti & Weimerskirch 2002) suggests an inherited mechanism used for navigation. The initial dispersal movement of juvenile wandering albatrosses seem to be based on a first step encoded as a fixed flight direction, and later the ability to return to a geographical region of the ocean after wind dispersal (examples given in Figure 1). We found only limited overlap between breeding adults and juvenile foraging zones, suggesting either present or past direct interactions with adults that would force juveniles to leave the proximity of the breeding grounds (Weimerskirch et al. submitted). However, it is likely that the genetically encoded behaviour has been selected to avoid competition in the past (e.g. Clobert et al. 2001, Alerstam et al. 2003). This is also suggested by the strict foraging of young birds in waters that are much less productive than those exploited by adult birds.

The second and more mobile phase of dispersal in young wandering albatrosses probably corresponds to the period of learning when birds initially disperse in several directions, with their movement being strongly influenced by wind conditions, and perhaps in combination with a genetic program encoding preferred migration directions inherited by their parents (e.g. Berthold 1996, Weimerskirch and Wilson 2000).

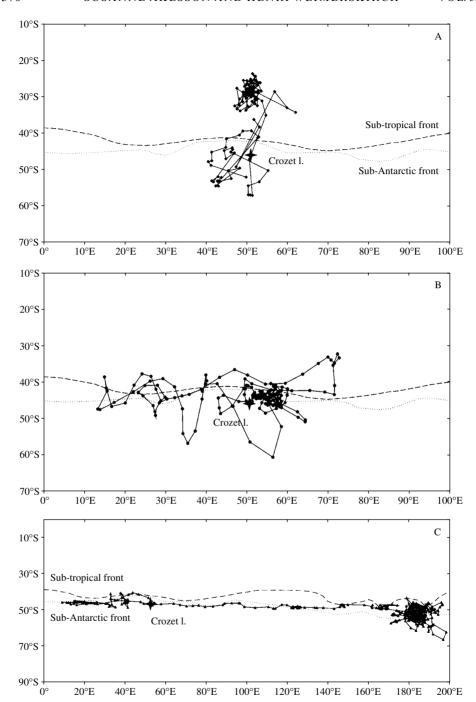


Figure 2. Examples of non-breeding movements of three (A–C) adult wandering albatrosses tracked by light intensity data loggers (Weimerskirch and Wilson 2000) and breeding at Crozet Islands. The location of the Crozet Islands is indicated by a star and the Sub-tropical and Sub-Antarctic fronts are indicated by broken and dotted lines, respectively. Modified after Weimerskirch and Wilson (2000).

After the first six months of independence when mobility has been acquired, birds will settle in more restricted geographical sectors of the ocean, noticeably in the Australian region (Figure 2c; Weimerskirch et al. submitted). It may be the first stage of the installation in what will be the area to which individual birds will return to during their future sabbatical years between two breeding seasons (Weimerskirch & Wilson 2000).

Our data indicates similarities between the first year dispersal movements in young wandering albatrosses and the migration to non-breeding destinations observed for adult birds. This suggests that this first period of dispersal explorations, guided at least in part by an inherited migration program and enabling the birds to return to previously visited areas of the ocean, are important for the migrations performed later in life. Still little is known about the cues that are used to guide the albatrosses during these long migrations (e.g. Papi and Luschi 1996, Åkesson 1996, 2003, Bonadonna et al. 2003a). We believe a combined effort using experimental paradigms (e.g. Kenyon and Rise 1958, Dall'Antonia et al. 1995, Papi et al. 2000, Luschi et al. 2001, Åkesson et al. 2003, Hays et al. 2003, Benhamou et al. 2003, Bonadonna et al. 2003c, Mouritsen et al. 2003) and tracking of natural migrations (e.g. Papi et al. 2000, Weimerskirch and Wilson 2000, Croxall et al. 2005, this study) will be necessary to disentangle the components of an inherited migration program and the acquired navigation tools guiding the birds during these long migrations across open sea in order to explain the spectacular long-distance migrations of albatrosses.

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REFERENCES

Able, K. P. 2001. The concepts and terminology of bird navigation. J. Avian Biol. 32: 174-183.

Åkesson, S. 1996. Geomagnetic map used for long-distance navigation? Trends Ecol. Evol. 11: 398-400.

Åkesson, S. 2003. Avian long-distance navigation: experiments with migratory birds. In: *Bird Migration* (Eds. P. Berthold and E. Gwinner), 471–492. Springer-Verlag, Heidelberg.

Åkesson, S. and Alerstam, T. 1998. Oceanic navigation: are there any feasible geomagnetic bi-coordinate combinations for albatrosses? *J. Avian Biol.* **29**, 618–625.

Åkesson, S., Broderick, A. C., Glen, F., Godley, B. J., Luschi, P., Papi, F. and Hays, G. 2003. Navigation by green turtles: which strategy do displaced adults use to locate Ascension Island? *Oikos* 103, 363–372.

Alerstam, T., Hedenström, A. & Åkesson, S. 2003. Long-distance migration: evolution and determinants. *Oikos* 103, 247–260.

Benhamou, S., Bried, J., Bonadonna, F. and Jouventin, P. 2003. Homing in pelagic birds: a pilot experiment with white-chinned petrels released in the open sea. *Behav. Proc.* 61, 95–100.

Berthold P. 1996. Control of Bird Migration. Chapman & Hall, London.

Boles, L. C. and Lohmann, K. P. 2003. True navigation and magnetic maps in lobsters. *Nature*, London 421, 60–63.

Bonadonna, F and Bretagnolle, V. 2002. Smelling home: a good solution for burrowfinding in nocturnal petrels? *J. Exp. Biol.* **205**, 2519–2523.

Bonadonna, F. and Nevitt, G. A. 2004. Partner-specific odour recognition in an Antarctic seabird. *Science* **306**, 835.

Bonadonna, F., Benhamou, S., and Jouventin, P. 2003a. Orientation in "featureless" environments: the extreme case of pelagic birds. In: *Bird Migration* (Eds. P. Berthold and E. Gwinner), 367–377. Springer-Verlag, Heidelberg.

- Bonadonna, F., Cunningham, G. B., Jouventin, P., Hesters, F. and Nevitt, G. A. 2003b. Evidence for nest-odour recognition in two species of diving petrel. *J. Exp. Biol.* **206**, 3719–3722.
- Bonadonna, F., Chamillé-Jammes, S., Pinaud, D. and Weimerskirch, H. 2003c. Magnetic cues: are they important in black-browed albatross *Diomedea melanophris* orientation? *Ibis*, **145**, 152–155.
- Bonadonna, F., Spaggiari, J. and Weimerskirch, H. 2001. Could osmotaxis explain the ability of blue petrels to return to their burrow at night? *J. Exp. Biol.* **204**, 1485–1489.
- Clobert, J., Danchin, E., Dhondt, A. A. & Nichols, J. D. 2001. *Dispersal*. Oxford University Press, Oxford. Courtillot, V., Hulot, G., Alexandrescu, M., Le Mouel, J.-L. and Kirschvink, J. L. 1997. Sensitivity and evolution of sea-turtle magnetoreception: observations modelling and constraints from geomagnetic secular variation. *Terra Nova* 9, 203–207.
- Croxall, J. P., Silk, J. R. D., Phillips, R. A., Afanasyev, V. and Briggs, D. R. 2005. Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. *Science* 307, 249–250.
- Dall'Antonia, L., Dall'Antonia, P., Benvenuti, S., Ioalè, P., Massa, B. and Bonadonna, F. 1995. The homing behaviour of Cory's shearwaters (*Calonectris diomedea*) studied by means of a direction recorder. J. Exp. Biol. 198, 359–362.
- Dingle, H. 1996. Migration: The biology of life on the move. Oxford University Press, Oxford.
- Dusenbery, D. B. 1992. Sensory Ecology. Freeman, New York.
- Fischer, J. H., Freake, M. J., Borland, S. C., and Phillips, J. B. 2001. Evidence for the use of a magnetic map by an amphibian. *Anim. Behav.* 62, 1–10.
- Grubb, T. C. 1972. Smell and foraging in shearwaters and petrels. Nature, London 237, 404-405.
- Hays, G. C., Åkesson, S., Broderick, A. C., Glen, F., Godley, B. J., Papi, F. & Luschi, P. 2003. Island finding ability in marine turtles. *Proc. R. Soc. Lond. B* (suppl.) Biol Lett. (DOI 10.1098/rsbl.2003.0022).
- Kenyon, K. W. and Rice, D. W. 1958. Homing in Laysan albatrosses. Condor 60, 3-6.
- Inchausti P. & Weimerskirch H. 2002. Dispersal and metapopulation dynamics of an oceanic seabird, the wandering albatross, and its consequences for its response to long-line fisheries. *J. Anim. Ecol.* 71, 765–770.
- Lednor, A. J. 1982. Magnetic navigation in pigeons: Possibilities and programs. In: *Avian Navigation* (Papi, F. and Wallraff, H. G., eds.), 109–119. Berlin: Springer-Verlag.
- Lequette, B., Verheyden, C. and Jouventin, P. 1989. Olfaction in sub-Antarctic seabirds: its phylogeny and ecological significance. *Condor* **91**, 732–735.
- Lohmann, K. J. and Lohmann, C. M. F. 1994. Detection of magnetic-inclination angle by sea-turtles a possible mechanism for determining latitude. *J. Exp. Biol.* **194**, 23–32.
- Lohmann, K. J. and Lohmann, C. M. F. 1996a. Orientation and open-sea navigation in sea turtles. *J. Exp. Biol.* **199**, 73–81.
- Lohmann, K. J. and Lohmann, C. M. F. 1996b. Detection of magnetic field intensity by sea turtles. *Nature* **380**, 59–61.
- Lohmann, K. J. and Lohmann, C. M. F. 1998. Migratory guidance mechanisms in marine turtles. *J. Avian Biol.* **29**, 585–596.
- Lohmann, K. J., Cain S. D., Dodge S. A. and Lohmann C. M. F. 2001. Regional magnetic field as navigational markers for sea turtles. *Science* **294**, 364–366.
- Luschi, P., Åkesson, S., Broderick, A. C., Glen, F., Godley, B. J., Papi, F. and Hays, G. 2001. Testing the navigational abilities of oceanic migrants: displacement experiments on green sea turtles (*Chelonia mydas*). Behav. Ecol. Sociobiol. 50, 528–534.
- Mouritsen, H., Huyvaert, K. P., Frost, B. J. and Anderson, D. J. 2003. Waved albatrosses can navigate with strong magnets attached to their head. *J. Exp. Biol.* **206**, 4155–4166.
- Nevitt, G. A. 1999. Olfactory foraging in Antarctic seabirds: a species-specific attraction to krill odours. *Mar. Ecol. Prog.* Ser. 177, 235–241.
- Nevitt, G. A. 2000. Olfactory foraging by Antarctic procellariiform seabirds: life at high Reynolds numbers. *Biol. Bull.* 198, 245–253.
- Nevitt, G. A., Veit, R. R. and Kareiva, P. 1995. Dimethyl sulphide as a foraging cue for Antarctic procellariiform seabirds. *Nature*, London 376, 680–682.
- Papi, F. 1992. General aspects. In: Animal Homing (Papi, F. ed), 1-18. Chapman & Hall, London.
- Papi, F. and Luschi, P. 1996. Pinpointing 'Isla Meta': the case of sea turtles and albatrosses. *J. Exp. Biol.* **199**, 65–71.
- Papi, F., Luschi, P., Åkesson, S., Capogrossi, S. and Hays, G. C. 2000. Open-sea migration of magnetically disturbed sea turtles. *J. Exp. Biol.* **203**, 3435–3443.

- Phillips, J. B. 1996. Magnetic navigation. J. theor. Biol. 180, 309-319.
- Skiles, D. D. 1985. The geomagnetic field; its nature, history and biological relevance. In: *Magnetite Biomineralization and Magnetoreception in Organisms* (Eds. J. L. Kirschvink, D., S. Jones and B. J. MacFadden), 43–102. New York, Plenum Press.
- Walker, M. M. 1998. On a wing and a vector: a model for magnetic navigation by homing pigeons. *J. theor. Biol.* **192**, 341–349.
- Wallraff, H. G. 1990. Conceptual approaches to avian navigation systems. Experientia 46, 379–388.
- Wallraff, H. G. 1999. The magnetic map of homing pigeons: an evergreen phantom. *J.theor. Biol.* 197: 265–269.
- Warham, J. 1990. The petrels: their ecology and breeding systems. Academic Press, London.
- Wehner, R. 1998. Navigation in context: grand theories and basic mechanisms. J. Avian. Biol. 29, 370-386.
- Weimerskirch H. & Wilson R. P. 2000. Oceanic respite for wandering albatrosses. Nature 406, 955-956.
- Weimerskirch, H., Åkesson, S., and Pinaud, D. submitted. Postnatal dispersal of wandering albatrosses: implications for the conservation of the species.
- Weimerskirch H., Jouventin P., Mougin, J. L., Sthal, J. C. and Van Beveren, M. 1985. Banding recoveries and dispersion of seabirds breeding in French austral and Antarctic territories. *Emu* 85, 22–23.
- Weimerskirch H., Salamolard M., Sarrazin F. & Jouventin P. 1993. Foraging strategy of the wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk* 110, 325–342.
- Wiltschko, R. and Wiltschko, W. 1995. *Magnetic Orientation in Animals*. Springer-Verlag, Berlin, Heidelberg.