

# COURTSHIP BEHAVIOUR OF THE WANDERING ALBATROSS *DIOMEDEA EXULANS* AT BIRD ISLAND, SOUTH GEORGIA

S.P.C. PICKERING & S.D. BERROW<sup>1</sup>

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

<sup>1</sup>Current address: Shannon Dolphin and Wildlife Foundation, Merchants Quay, Kilrush, Co. Clare, Ireland  
(SDWF@oceanfree.net)

Received 1 November 1999, accepted 13 January 2001

## SUMMARY

PICKERING, S.P.C. & BERROW, S.D. 2001. Courtship behaviour of the Wandering Albatross *Diomedea exulans* at Bird Island, South Georgia. *Marine Ornithology* 29: 29–37.

The behaviour postures and their sequences during courtship displays of the Wandering Albatross *Diomedea exulans* at South Georgia are described. Females initiated most display bouts, which began with a series of greetings. The core of the display consisted of a rapid sequence of head movements, snaps, ritualized preening and vocalisations. Most display bouts ended when the female walked away, although in 25% of cases the birds sat together on the male's nest site. An underlying basic sequence was common to both sexes although there were differences in responses to the partner's behaviour. Courtship behaviour was very similar to that described for Wandering Albatrosses breeding in the Indian Ocean.

Key words: Wandering Albatross, *Diomedea exulans*, South Georgia, courtship, behaviour

## INTRODUCTION

Amongst seabirds, albatrosses are renowned for their complex visual and vocal displays with behavioural repertoires tending to be most complex in large, long-lived species (Warham 1996, Tickell 2000). The elaborate courtship display of the Wandering Albatross *Diomedea exulans* was first noted by Matthews (1929) and Murphy (1936) but has only recently been fully described (Jouventin & Lequette 1990, Lequette & Jouventin 1991a). Warham (1996) suggested that the behavioural repertoire of the Wandering and the Royal Albatross *D. epomophora* were basically similar; however, descriptions of courtship of both species are from a limited number of sites and detailed comparisons are few (Richdale 1950, Lequette & Jouventin 1991b).

In this study we describe the courtship behaviour of Wandering Albatrosses breeding at South Georgia in the South Atlantic. We present an analysis of the sequence and context in which each type of behaviour is performed and compare it to similar information from Iles Crozet in the southern Indian Ocean.

## METHODS

The study was carried out on Wanderer Ridge, Bird Island, South Georgia (54°S, 38°W), during three austral summers (December to March) 1983/84 to 1985/86. Most of the detailed results presented here were obtained during the 1984/85 season. The topography, vegetation and climate of the study area are described by Hunter *et al.* (1982) and full details of the study population are

given in Pickering (1989). Each breeding season during the study, approximately 300 non-breeding birds (birds that have never bred before) and 100 former breeders (birds that have previously bred but are not breeding that season) visit the study area. Virtually all birds are individually identified with numbered monel rings and numbered (or alpha-numeric) coloured Darvic rings and most (>95%) of the non-breeding birds are of known age. Birds were sexed on size and plumage (males are larger and have lighter plumage, Tickell 1968). Observations concentrated on individual birds for which there was information on attendance patterns and behaviour in the previous seasons.

Observations were made in late afternoon each day throughout the breeding season. Each behaviour posture was photographed on black-and-white film to provide a reference collection. Field descriptions of 517 courtship bouts were tape recorded and later transcribed. Data on the sequence of behaviours were obtained by video-recording 72 display bouts (using a JVC Neveikon GX-N70E camera) and subsequently analysing these in detail.

The sequence in which behaviours were performed was analysed by arranging the data in a transition matrix. For this the number of times each behaviour followed another was recorded. The identity of each bird was taken into account which resulted in four separate matrices, one each for female to female, male to male, female to male and male to female transitions. In order to reduce the number of cells that contained zeros, each axis was reduced to 14 behaviours (total number of transitions = 10 393). Those behaviours dropped from the analysis were either rare or those performed only at the beginning and/or end of a display bout. A

modified chi-squared test (Fagen & Young 1980) was used to test for significance.

## RESULTS

### Individual display postures

The fieldwork for this study was carried out before the recent papers on courtship in Wandering Albatrosses by Jouventin & Lequette (1990) and Lequette & Jouventin (1991a) and the reviews by Warham (1996) and Tickell (2000). As far as possible consistency with the nomenclature used by these authors has been retained, referencing Tickell (2000) in all cases.

A total of 22 distinct behavioural acts was identified during courtship: 12 directed towards the display partner (seven of which were accompanied by vocalisations), five head movements, three ritualised preening activities and two locomotory acts. These were described as follows:

#### *Allo-preening*

Allo-preening (AP) (Fig. 1) was normally directed towards the head, neck or breast feathers and was frequently performed by paired birds or those in an advanced stage of pair bond formation as distinct from Auto-Preening (PR).

#### *Pointing*

When Pointing, the bird stretches its head and neck rigidly towards a partner (Tickell 2000). Pointing was sub-divided into Head Forward Low (FL) (Fig. 2a) which was usually directed to the partner's breast ('Breast Billing' of Jouventin & Lequette, 1990) and Head Forward High (FH) (Fig. 2b) which was normally directed to the partner's bill (similar to 'Bill Pointing' in Warham (1996), where the male's head is slightly higher than the female's). Pointing may become synchronised with the extended bills of two birds being held close, often touching each other (Touch Beaks (TB), Fig. 2c) and frequently ends with a pronounced Snap. We also used Bill Nibble (BN) when one bird gently nibbles the side of the other's bill.

#### *Rattle*

Mandibles are Rattled (R) or vibrated rapidly through shallow arcs and volleys of loud, pulsed, rubbery sounds and the head is drawn back and slowly raised (Fig. 3).

#### *Head Roll*

We used the term Head Roll (HR) instead of 'Arched Neck' (Jouventin & Lequette 1990), for the movement of the head backwards and down while the bill is tucked in towards the neck then thrust rapidly up and forward, stretching the neck out (Figs 4a & 4b).

#### *Snap*

Single bill Snaps (SN) occur when mandibles are snapped together smartly without a forward lunge, often into the air. The sound produced resembles that made by striking two pieces of wood together.

#### *Sky Point*

In Sky Point (SP), termed 'Sky-Position' by Jouventin & Lequette (1990), the head is lowered slightly then swung to the near vertical (70–90° from horizontal, Fig. 5a). This can be performed from a sitting or standing position and is essentially a quiet action but may be accompanied by a deep, guttural, gurgling noise when performed vigorously.

#### *Sky Call*

Sky Call (SK) is a much more excitable performance ('Sky-Position-Call' by Jouventin & Lequette, 1990, 'Head, Shake and Whine' by Warham, 1996) when the head is swung up with opened beak so that the head and neck are at 45° or more and a series of vocalisations are emitted with the head and bill motionless but often with wings outstretched (Fig. 5b). A rapid inhalation with distinct harmonics followed by a loud scream accompanies the Sky Call which Jouventin & Lequette (1990) termed 'Whine' and Warham (1996) 'Wing Stretch'. Although birds sometimes gave only one scream it was more typical to perform between two and five Sky Calls in succession. The second Sky Call was normally performed immediately after the first but subsequent Sky Calls were usually separated by Yammering.

#### *Bowing*

Bowing is a rapid movement when the bird swings its head down towards its feet, often touching its lower breast and, if standing, may reach between its legs; it is highly variable sometimes involving just the head (nod) but usually more of the body is involved. We sub-divided this behaviour into Head Bob (HB) (Fig. 6a) when the bird stopped 10–20 cm above the ground and Head Curl (HC) (Fig. 6b) when the head was twisted to the side bringing one eye facing forward towards the display partner and the other towards the bird's own feet.

#### *Side Preen*

A standing bird raises its head quickly, makes a single Snap, then plunges its bill into the feathers on one side of the breast (SNPR, Fig. 7a). This behaviour was called 'Scapular Action' by Jouventin & Lequette (1990) and 'Leg Action' by Warham (1996).

#### *Front Preen*

Front Preen (PB) has less movement; the bill preens feathers of the upper breast or the neck (Fig. 7b).

#### *Flagging*

In Flagging a bird walks upright turning its head from side to side (Head Wag – HW). Head Shake (HS, Fig. 8) describes when the head is jerked from side to side horizontally so that the mandibles rattle loosely together.

#### *Yammering*

Yammering (YM) is an aggressive act when the bird stretches its neck and head, utters a powerful call and violently claps its mandibles at about 10 claps per second and is often directed at an intruder without any movement (Fig. 9).

### Yapping

Yapping (YA) is used to describe up and down head motions and slightly opened bill (Fig. 10) uttering gruff *waa-waa-waa* vocalisations at about 2–3 *waas* per second. This behaviour was typically performed by a bird sitting on a nest site. Jouventin & Lequette (1990) used 'Duet' to define partners simultaneously Yapping.

In addition to these stereotyped behaviours, two locomotory behaviours were also recognised. During courtship bouts birds often Walk Around (WA) each other, typically with a rolling gait with their heads and necks stretched forward horizontally. Birds sometimes walk upright with their head up and without this exaggerated swaying which was termed 'Sway Walk' by Warham (1996). We also used Walk to Nest site (WTN) when birds stopped displaying and the female followed the male back to his nest site where they would continue to display and/or sit Yapping.

### General courtship behaviour

Courtship displays normally involved unpaired birds in the process of finding a mate. Only very occasionally did paired or breeding birds perform full courtship displays. Young non-breeding birds visited the display areas throughout the day, with numbers peaking in early evening and males tended to arrive earlier in the season than did females (Pickering 1989). Once ashore, established males spent most of their time on their nest sites, whereas less experienced males frequented popular display areas or leks. By their third season most of these males had established a nest site close to one of these display areas.

When arriving in the study area, females did not normally land immediately but made several low level passes over the display areas before landing. This pattern of making several passes, over display areas was much less common amongst males and tended to be restricted to inexperienced birds. During strong winds (>45 km/h) females made slow passes occasionally hanging on the

wind above a male. On several occasions a female was observed to touch beak with a Sky Pointing male before landing or flying on.

After landing a female would walk, with a low rolling gait, towards a male. A female would often walk past several males before displaying. Females initiated 80.1% of display bouts ( $n = 414$ ) and males 19.9% ( $n = 103$ ). Most began with a female walking up to a male on his nest site. Occasionally males would approach females or try to join in display bouts. As a female approached a male she would sometimes stop and Sky Point; in response the male would also Sky Point. Pointing was the most frequently recorded behaviour accounting for 38% of all interactions. Most displays began with a sequence of Head Forward High, Head Forward Low, Bill Touch, Bill Snap, Head Bob and Head Curl. Many display bouts did not progress beyond this greeting stage.

After greeting, the rate and the number of behaviours increased with birds performing Rattle, Head Roll and Side Preen in addition to the greeting behaviours. Whereas these behaviours were used in virtually all display bouts, Sky Calls were only performed in 26.2% of display bouts. Bouts of continuous display lasted from a few seconds to 15 minutes with most bouts lasting between two and six minutes (mean  $\pm$  SE,  $4.2 \pm 0.4$  m,  $n = 58$ ). Display bouts in which one or more birds Sky Called were significantly longer ( $5.1 \pm 0.5$  min) than bouts in which no birds Sky Called ( $2.9 \pm 0.4$  min) ( $t = 3.08$ ,  $P < 0.01$ ).

When a bird Sky Called, its display partner(s) would often try to pirouette around the calling bird. This would force the Sky Calling bird to turn around with its wings open so as to continue facing its display partner(s). Sometimes birds would walk towards their Sky Calling display partner. This usually caused the Sky Calling bird to walk backwards. Females frequently performed Head Forward Low towards Sky Calling males and would sometimes peck at the male's breast feathers, occasionally pulling some of them out. Both sexes Sky Called and there was no sex bias in which bird Sky Called first or most frequently. Displaying birds

TABLE 1

The cause of display bouts ending by male and female Wandering Albatrosses

How display bout ends	Number	%
Site as a pair at a nest site	131	25.3
Male ends display bout:		
Male walks off	18	3.5
Male drives female(s) away	9	1.7
<b>Total</b>	<b>27</b>	<b>5.2</b>
Female ends display bout:		
Female walks off	329	63.6
Another female approaches; original female walks off	11	3.7
Another male approaches and female walks off	19	2.1
<b>Total</b>	<b>359</b>	<b>69.4</b>

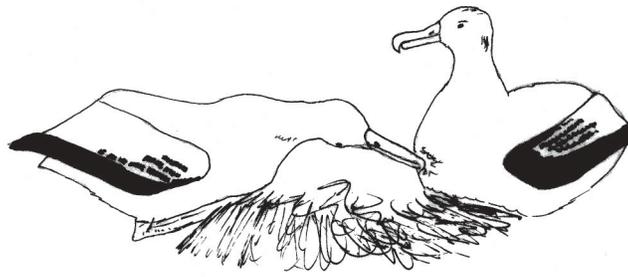
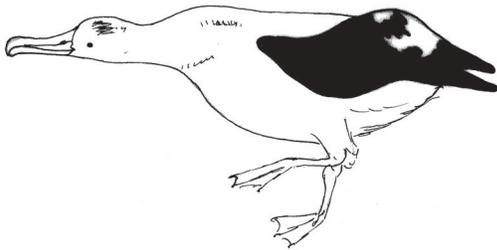
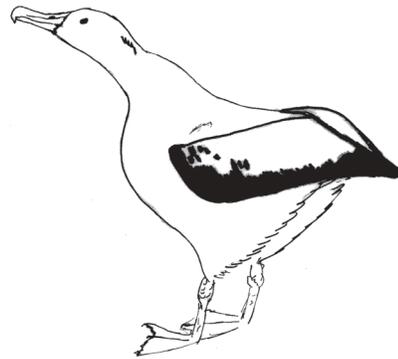


Fig. 1. Allo-preening (AP).

2a



2b



2c

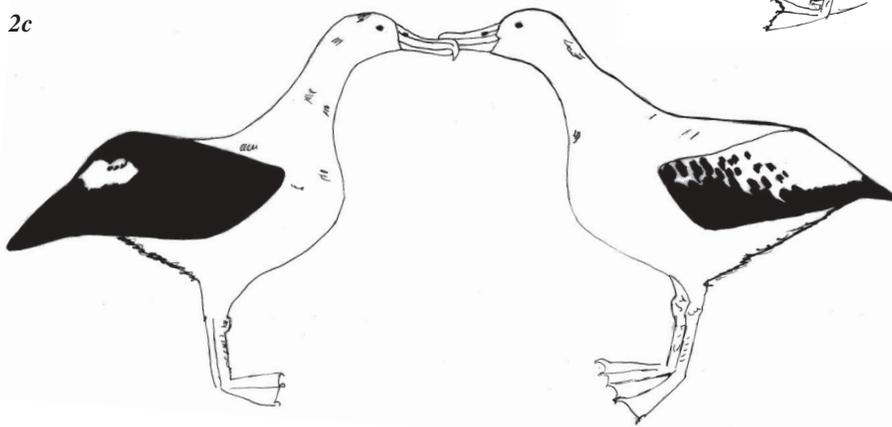
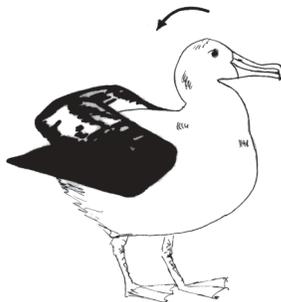


Fig. 2. Pointing: (a) Head Forward Low (FL), (b) Head forward High (FH), (c) Touch beaks (TB).



Fig. 3. Rattle (R).

4a



4b

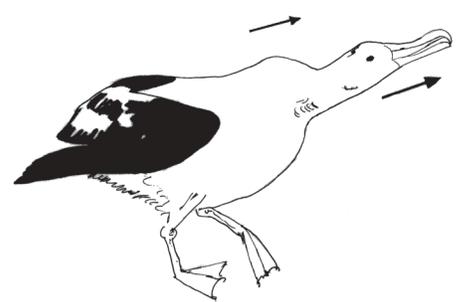
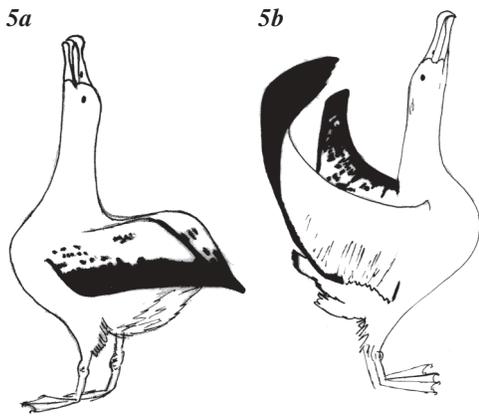
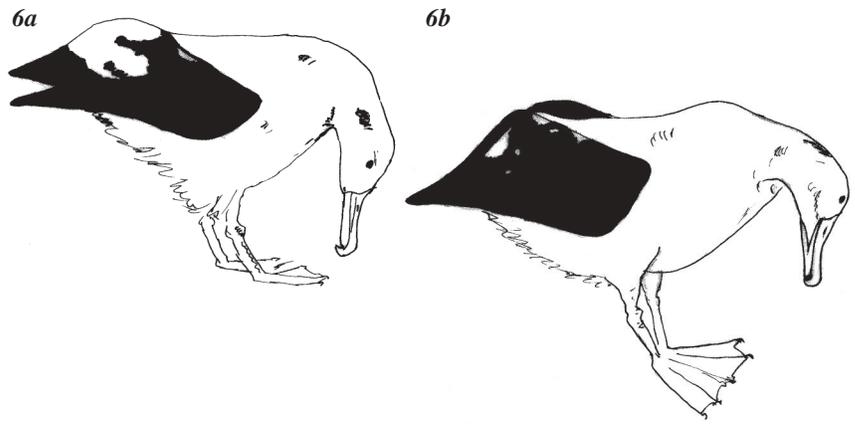


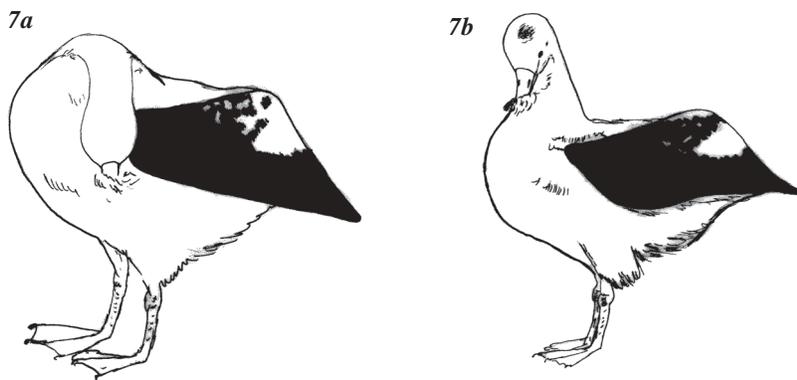
Fig. 4a & 4b. Head Roll (HR).



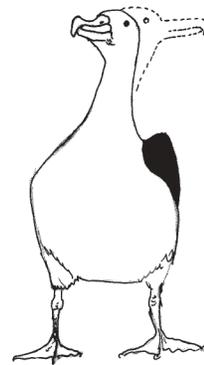
**Fig. 5.** Calling: *(a)* Sky Point (SP), *(b)* Sky Call (SK).



**Fig. 6.** Bowing: *(a)* Head Bob (HB), *(b)* Head Curl (HC).



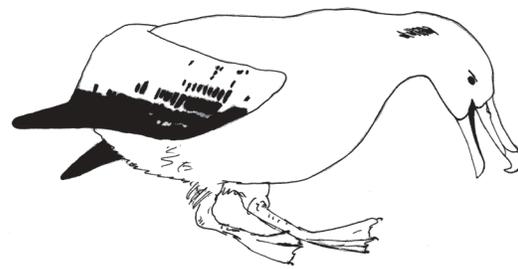
**Fig. 7.** Preening: *(a)* Side preen (PW), *(b)* Front Preen (PB).



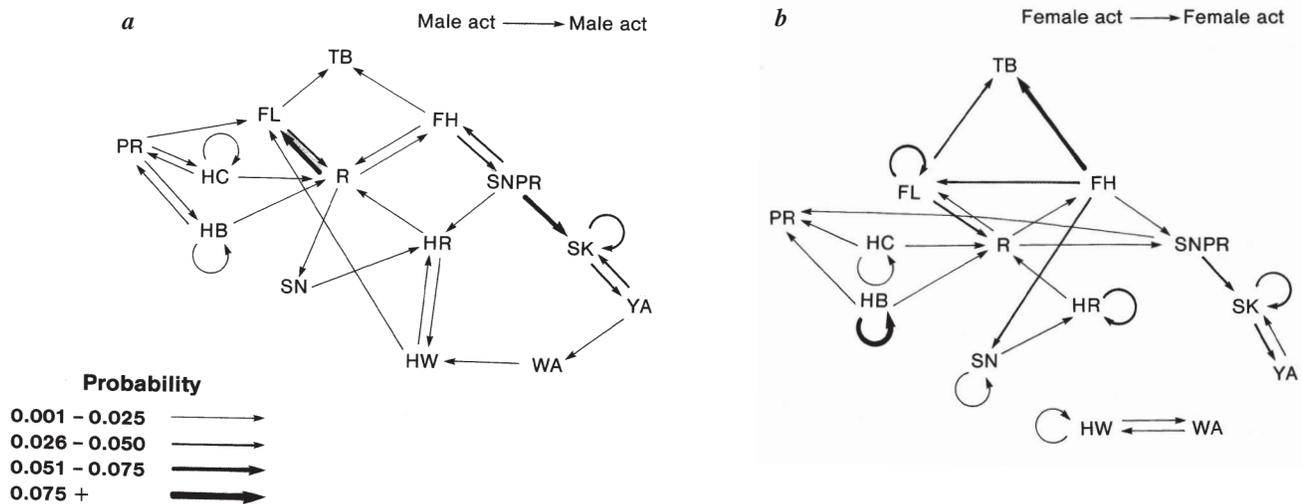
**Fig. 8.** Head Shake (HS).



**Fig. 9.** Yammering (YM)



**Fig. 10.** Yapping (YA).



**Fig. 11.** Flow diagram to illustrate the significant transitions of (a) male behavioural acts, (b) female behavioural acts. The thickness of the lines is proportional to the probability of the transitions occurring. See text for display names.

sometimes Sky Called in large display groups and it was not uncommon for two or three birds to Sky Call together.

The majority of display bouts (69.4%) ended when the female(s) walked away (Table 1). Females were observed to walk away from males at any point during a display bout. However, in most display bouts the rate of display gradually decreased and both birds performed a series of Head Bobs before the female walked off. A quarter of display bouts ended with the female following the male back to his nest site (Table 1). Established males would nearly always walk back to their nest site after a display bout and begin to Yapping. If a female followed she would sometimes sit by the side of the nest site watching the male and sometimes would join in with the male Yapping. Pairs of birds sitting Yapping together frequently stopped and preened each other. Females often snapped at males attempting to preen them. Normally males continued to attempt to preen the female; sometimes, however, they would snap at the female, occasionally attacking and driving her away. After a period of Yapping and preening at a nest site, some pairs (32.2%,  $n = 131$ ) began the display again before the female eventually walked off to display with another male or flew out to sea. Only paired females remained with the male overnight or until the male left the island just before dusk.

### Fighting

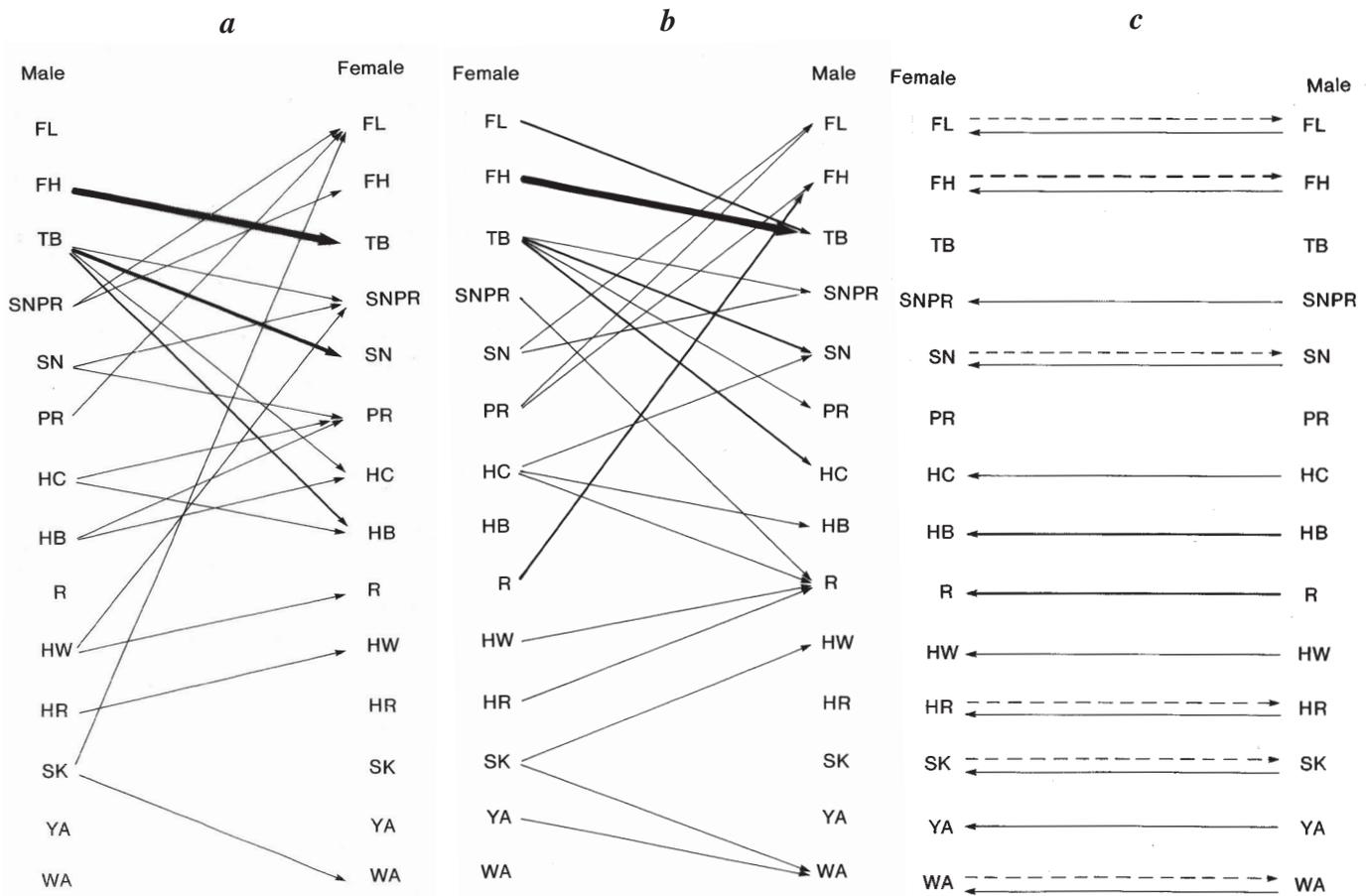
Disputes over nest sites by males and over display partners by females occasionally resulted in fights. If a male approached another's nest site the owner normally Yammered at the intruder who withdrew. The distance from the nest site at which an intruder would be attacked varied considerably but virtually all males within 1 m of an occupied nest site would be Yammered at. As the intruder withdrew, the nest site owner frequently performed a series of Sky Points. Intruding males would sometimes return the Yammer before withdrawing. This would normally provoke another Yammer and occasionally a charge by the nest site owner; if the intruder did not withdraw fights often developed. Wandering Albatrosses fight by snapping at their opponent's head and neck and shake it vigorously if they get a firm hold on part of their opponent, e.g. head, neck or wing.

Fights normally lasted only a few seconds and although injuries were rare, two fights were observed where one bird hooked its beak into the eye sockets of its opponent causing considerable bleeding. One of these fights was between two breeding males in the pre-lay period and the other between two females displaying with the same male. Although females displaying with the same male would often snap at each other fights were rare. When females did fight they tended to engage in short violent clashes interspersed with displaying with the male. Males normally avoided these disputes which could continue for up to 20 minutes.

### Sequence analysis

Out of a possible 730 transitions, 632 were observed but only 115 were statistically significant at the 0.01 probability level. The sequence of behaviours between males are presented in Fig. 11a and between females in Fig. 11b. There were 29 significant male–male transitions and 26 significant female–female transitions of which 21 were common to both sexes. Rattle–Head Forward Low and Side Preen–Sky Call were the most frequent transitions ( $P > 0.075$ ) by a male to a male followed by Head Forward High–Touch Beaks, Head Forward Low–Rattle and Sky Call–Yapping (Fig. 11a). Head Forward High–Touch Bills and Head Bob–Head Bob the most frequent female to female transition ( $P > 0.075$ ) followed by Head Forward Low–Rattle, Head Forward High–Snap, Side Preen–Sky Call, Sky Call–Yapping and Head Forward Low–Touch Beaks (Fig. 11b). Excluding repeats of the same behaviour, most were common to both males and female birds, indicating that the underlying pattern of display is similar for both sexes.

There were 34 significant male–female transitions (Fig. 12a) and 32 significant female–male transitions (Fig. 12b). Head Forward High–Touch Beaks was the most frequent male to female and female to male transition followed by Touch Beaks–Snap (male–female). Of these, 18 were common to both, i.e. 56% of female and 59% of male responses were the same (Fig. 12c). A significantly greater proportion of all male–female transitions (34%) than of female–male transitions (14%) were of the second bird performing behaviour that the first had just performed ( $\chi^2_1 = 195.0$ ,  $P < 0.001$ ).



**Fig. 12.** Flow diagram to illustrate the significant transitions from (a) male to female behaviour, (b) female to male behaviour, and (c) where the behavioural acts are the same between the sexes. See text for display names.

## DISCUSSION

Pair formation in Wandering Albatrosses at South Georgia may extend over many years; however, once paired, birds are faithful to their partner (Pickering 1989). The complex courtship displays of Wandering Albatrosses are important in establishing compatibility between birds and forging a long-lasting bond (Warham 1996). There are strong links between visual and acoustic signals, leading to stereotyped characteristics which have often been described as a 'dance' (Jouventin & Lequette 1990, Lequette & Jouventin 1991a).

### Function of displays

The possible function of behavioural postures during courtship by Wandering Albatrosses was discussed by Jouventin & Lequette (1990) and summarised by Warham (1996) and Tickell (2000).

Pointing is the most frequently recorded action between courting albatrosses both at South Georgia and Iles Crozet, accounting for 32% of interactions (Jouventin & Lequette 1990) and is often used as a greeting or as the prelude to more intense activity (Tickell 2000). Touch Beaks is the only mutual behaviour requiring both birds to perform the same actions together. Females most frequently responded to a Touch Beaks with a Snap which is clearly

an aggressive behaviour. However, males followed a Touch Beak with Bowing which is thought to represent appeasement (Warham 1996).

Rattle was the third most frequently performed behaviour at South Georgia and at Iles Crozet (Jouventin & Lequette 1990). It was typically performed after a Head Bob, Head Roll or Head Forward Low. It did not appear to be either an aggressive or appeasement behaviour; Lequette & Jouventin (1991a) thought it conveyed intention to contact the partner.

The Sky Call has two components, the physical movements and the vocalisation. The physical movements resemble a vigorous Sky Point with the wings held outstretched; however, these two behaviours were used in very different contexts at South Georgia. The Sky Point was performed by males to a female flying overhead or walking past and by both sexes during or after aggressive encounters. In the latter situations it appears to indicate some form of threat or display of size or dominance whereas in the former it appears simply to express the male's interest in the passing female (Warham 1996). The Sky Call was usually performed in the middle of display bouts after which the rate of display usually declined. The outstretched wings may have originally been used to help balance, birds frequently using their wings for balance when walking across difficult terrain. However, Sky Calling birds may

also be demonstrating their overall size to their display partner which is accentuated by outstretched wings. No aerial Sky Calls, such as described by Lequette & Jouventin (1991b) were recorded.

A Sky Call was virtually always followed by another Sky Call or by Yammering. Yammering performed in this situation is virtually indistinguishable from Yammering used when defending a nest site or attacking another bird. Yammering is overtly aggressive while the Sky Call itself does not appear to represent an aggressive intention. In fact, a Sky Calling bird exposes its neck and chest and is vulnerable to attack from a display partner. Interestingly the aggressive Yammering display of Wandering Albatrosses seems rarely to be performed by Royal Albatrosses (Lequette & Jouventin 1991b). Females frequently performed a Head Forward Low to a Sky Calling male and may peck his breast feathers. Both males and females try to walk around a Sky Calling bird or even force them to walk backwards. This may be birds attempting to see the dorsal surface of the wing in order to assess their age (Gibson 1967). The exaggerated Head Wagging performed as birds walk around each other may have developed from the need for a bird to turn its head to get a complete view of its partner.

As pair-bonds develop between birds they spend less time displaying and more time sitting together Yapping (Pickering 1989). This simultaneous Yapping or 'Duet' may be particularly important in strengthening the pair-bond as it could be used for individual recognition (Warham 1996).

### Comparison with other albatrosses

When transitions between display postures are compared with that reported for Wandering Albatrosses at Iles Crozet (Jouventin & Lequette 1990) greater consistency occurred in male to male interactions. Rattle-Pointing were highly significant transitions at both sites and Pointing-Side Preen was also frequent. In female to female interactions only Sky Call-Yammering and Bill Snaps-Sky Call were significant at both sites. There were few significant transitions ( $P > 0.05$ ) between sexes at South Georgia (three male to female and four female to male) and none were the same as reported from Iles Crozet. However, the basic transitions, successions and dialogues (Jouventin & Lequette 1990) were very similar.

Studies of the smaller albatrosses are few and details only available for the mollymawks *Thalassarche* spp. and the sooty albatrosses *Phoebastria* spp. (Warham 1996, Tickell 2000). Common to all species of albatrosses studied is some form of Head Forward movement and Bill Touch (e.g. Rice & Kenyon 1962, Tickell 1984). All mollymawks, except Sooty Albatrosses *Phoebastria fusca*, perform a form of Yapping or croaking, particularly when at a nest site. They all allo-preen their display partner or potential breeding partner, include a form of Snap in their repertoire and move their head and bill as if to preen the body feathers by the wing.

The only movement with any close resemblance to the Head Roll performed by Wandering Albatrosses is the Head Flick performed by Laysan *Phoebastria immutabilis* and Black-footed *P. nigripes* Albatrosses (Fisher 1972). These North Pacific species also perform a form of Rattle which is absent from the repertoire of the mollymawks in the Southern Hemisphere. The Sky Call per-

formed with wing held out appears to be restricted to the larger albatross species. However, both Black-footed and Laysan Albatrosses perform a Sky Call during courtship but with closed wings (Fisher 1972, Meseth 1975). The Sky Moo of these North Pacific species and the Sky Call (chant) of the Sooty Albatross appear to be performed to advertise the presence of a bird, typically the male, in the same way as Wandering Albatrosses use the Sky Point.

Overall, the courtship behaviour repertoire of the Wandering Albatross appears to have more in common with that of Laysan and Black-footed Albatrosses than with Black-browed *Thalassarche melanophris*, Grey-headed *T. chrysostoma* or Sooty Albatrosses. It is unclear whether this is due to a closer phylogenetic relationship between Wandering Albatrosses and North Pacific albatrosses or to the topography of their breeding grounds. Black-footed, Laysan and Wandering Albatrosses all display and breed on relatively flat and open ground. In contrast, Black-browed, Grey-headed and Sooty Albatrosses typically nest on steep broken ground or cliffs, on which it may be impossible to perform the elaborate courtship 'dances' characteristic of the larger albatross species. The complex interactive courtship behaviour resulting in a form of dialogue developing between displaying Wandering Albatrosses is typical among albatrosses (Meseth 1975, Jouventin *et al.* 1981). In the season before breeding, paired birds spend much less time displaying than do unpaired birds (Pickering 1989). It seems likely that the complex courtship displays may allow birds, particularly females, which initiate and terminate most displays (Meseth 1975, Jouventin *et al.* 1981), to assess and re-assess the quality or compatibility of a potential partners before beginning the process of pair bond formation

### ACKNOWLEDGEMENTS

We thank John Croxall for initiating and providing constructive criticism throughout this study, Guy Beauchamp for assistance with the sequence analysis and Lance Tickell and John Warham for constructive comments on an earlier draft of this paper.

### REFERENCES

- FAGEN, R.M. & YOUNG, D.Y. 1978. Temporal patterns of behaviors: durations, intervals, halencies and sequences. In: Colgan P.W. (Ed.). Quantitative ethology. New York: John Wiley & Sons. pp. 79-114.
- FISHER, H.I. 1972. Sympatry of Laysan and Black-footed Albatrosses. *Auk* 89: 381-402.
- GIBSON, J.D. 1967. The Wandering Albatross (*Diomedea exulans*): results of banding and observations in New South Wales coastal waters and Tasman Sea. *Notornis* 14: 47-57.
- HUNTER, I., CROXALL, J.P., PRINCE, P.A. 1982. The distribution and abundance of burrowing seabirds (Procellariiformes) at Bird Island, South Georgia: 1. Introduction and methods. *British Antarctic Survey Bulletin* 56: 49-67.
- JOUVENTIN, P., DE MONICAULT, G. & BLOSSEVILLE, J.M. 1981. La danse de l'albatros, *Phoebastria fusca*. *Behaviour* 78: 49-80.
- JOUVENTIN, P. & LEQUETTE, B. 1990. The dance of the Wandering Albatross *Diomedea exulans*. *Emu* 90: 123-131.
- LEQUETTE, B. & JOUVENTIN, P. 1991a. The dance of the

- Wandering Albatross II: Acoustic signals. *Emu* 91: 172–178.
- LEQUETTE, B. & JOUVENTIN, P. 1991b. Comparison of visual and vocal signals of great albatrosses. *Ardea* 79: 383–394.
- MATTHEWS, G.V.T. 1929. The birds of South Georgia. *Discovery Reports* 1: 563–592.
- MESETH, E.H. 1975. The dance of the Laysan Albatross *Diomedea immutabilis*. *Behaviour* 54: 217–257.
- MURPHY, R.C. 1936. Oceanic birds of South America. New York: Macmillan & American Museum of Natural History.
- PICKERING, S.P.C. 1989. Attendance patterns and behaviour in relation to experience and pair bond formation in the Wandering Albatross *Diomedea exulans* at South Georgia. *Ibis* 131: 183–195.
- RICE, D.W. & KENYON, K.W. 1962. Breeding cycles and behavior of Laysan and Black-footed Albatrosses. *Auk* 79: 517–567.
- RICHDALE, L.E. 1950. The pre-egg stage in the albatross family. *Biological Monographs* (Dunedin, NZ) 3: 1–92.
- TICKELL, W.L.N. 1968. The biology of the great albatrosses *Diomedea exulans* and *Diomedea epomophora*. *Antarctic Research Series* 12: 1–55.
- TICKELL, W.L.N. 1984. Behaviour of Black-browed and Grey-headed Albatrosses at Bird Island, South Georgia. *Ostrich* 55: 64–85.
- TICKELL, W.L.N. 2000. Albatrosses. Mountfield, Sussex: Pica Press.
- WARHAM, J. 1996. The behaviour, population biology and physiology of the petrels. London: Academic Press.
-

