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What drives long-distance movements in the nomadic Grey Teal *Anas gracilis* in Australia?

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In contrast to northern temperate environments, where day length and temperature changes are obvious proximate cues for movement to resource-rich breeding habitats, the cues for movement used by birds in an often resource-poor, stochastic environment are less obvious. We recorded long-distance movements of 23 Grey Teal *Anas gracilis* using satellite telemetry for up to 879 days and examined the relationship between those movements and environmental factors, such as heavy rainfall and flooding, at the destination site. We identified 32 long-distance (> 150 km) movements that met our criterion for minimally interrupted flight between origin and destination. Thirteen of these flights coincided with rainfall and/or flooding events up to 1050 km from the origin. However, some ducks moved without any clear beneficial conditions at the destination onto small wetlands in regions with little surface water. The data suggest that there are two types of long-distance movement – ranging and directed. These flights occurred over distances up to 1200 km across the arid inland. The rates and distances of movement suggest that long-distance movements of Grey Teal entail high energy costs as in waterfowl elsewhere. We conclude that the proximate controls of directed movements need not be very different from those of their temperate counterparts.

Keywords: environmental cues, Grey Teal, migration, nomadism, satellite telemetry.

Many Australian waterfowl are wide ranging and dispersive and the Grey Teal *Anas gracilis* is often the exemplar avian nomad in analyses of movement and migration (Dingle 1996, 2006). Banding studies of waterfowl in Australia, including studies on Grey Teal, have shown that some individuals undertake movements of hundreds, sometimes thousands, of kilometres (Frith 1957, 1959, 1962, 1963, Lawler *et al.* 1993). As with long-distance seasonal migrants, these irregular movements are thought to be undertaken to exploit resources for breeding or survival (Kingsford & Norman 2002). In contrast to northern temperate environments, where changes in day length and temperature trigger hormonal changes in many species that act as proximate cues for migration to breeding habitats (Gwinner 1996), the cues for movement that birds use in a stochastic environment are less obvious. In a stochastic environment where wetland resources are mostly temporary and non-seasonally available (Kingsford *et al.* 1999, Roshier *et al.* 2001a, 2001b), endogenous control of movement and migration is less likely to facilitate exploitation of new resources.

Waterbirds in an arid environment must be able to detect directly or by proxy the presence of water and wetlands, else they perish. It has been suggested that waterbirds in these environments find temporary wetlands by visual cues and/or temperature and pressure gradients (Simmons *et al.* 1998). Whereas the former is almost certainly true at some scale, the distances travelled to reach temporary and widely distributed wetland resources and the true nature of the cues remain speculative. In Australia, changes in local abundance of waterbirds have been attributed to movement in response to flooding or extended drought in the arid interior of the continent (Frith 1957, 1959, 1962, Kingsford 1996, Roshier *et al.* 2002). With the advent of satellite telemetry, the nature and extent of movements and the environmental

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factors associated with movement and migration can now be explicitly investigated. In this paper, we report on the results from a study in which we used satellite telemetry to investigate the environmental conditions at the origin and destination of long-distance movements undertaken by Grey Teal. An earlier analysis of these data showed that individuals tended to move large distances between sites that they subsequently occupied for extended periods (Roshier *et al.* 2006). However, the environmental conditions at the origin and destination were unknown and the cues for movement speculative. In this analysis we used weather records and satellite imagery to correlate movement of this wetland-dependent species with either rainfall events or flooding. To better understand the timing of long-distance movements and directness of passage to new occupied sites, we tracked an additional four birds fitted with transmitters that pulsed continuously throughout the day and night. In total, we tracked 23 ducks for up to 879 days using satellite telemetry during which we recorded long-distance movements (> 150 km) and durations of stay at staging sites en route.

METHODS

Study species

Grey Teal are small-bodied (< 600 g) waterfowl that use a wide range of aquatic habitats but most favour large, often temporary, shallow inland wetlands that provide an abundance of food sources for a limited period (Marchant & Higgins 1990 and references therein). The Grey Teal is one of six closely related austral species, including two with which its geographic range overlaps, Chestnut Teal *Anas castanea* and Indonesian or Sunda Teal *Anas gibberifrons* (Kear & Hulme 2005). The most closely related northern temperate species is the Eurasian Teal *Anas crecca* (Young 1997). Their geographic range includes the whole of Australia, New Zealand, New Guinea and the islands of the Indonesian archipelago as far west as Java (Fullaghar 1992). Grey Teal are among the most dispersive of Australian waterfowl and have been recorded moving from south-eastern Australia to Western Australia and New Guinea (Frith 1957, 1982).

Study sites

We studied the movements of Grey Teal in the agricultural districts of the southern portion of the Murray-Darling Basin in eastern Australia and the desert landscapes of the Lake Eyre Basin in central Australia, *c.* 1000 km to the northwest (Fig. 1). Wetland habitats in the Murray-Darling Basin are varied and most of the larger wetlands have an altered hydrological regime as a result of diversion or extraction of water for agriculture (Kingsford 2000). In contrast, the Lake Eyre Basin is a vast (1 140 000 km^2) internally draining basin of varied landscapes. These include longitudinal sand dunes, hard gibber (stony) plains, large salt lakes, and broad floodplains associated with dryland rivers that flow south and west down shallow gradients toward terminal wetlands hundreds of kilometres to the south (Puckridge *et al.* 1998). The infrequent floods inundate vast areas (10^6 ha; Roshier *et al.* 2001a) and produce a diverse range of highly productive but mostly temporary wetland habitats for waterbirds and other biota (Puckridge *et al.* 1998, Sheldon *et al.* 2002, Bunn *et al.* 2003). The study area is described more fully in Roshier *et al.* (2006).

Satellite tracking

We used two types of light-weight (< 18 g) satellite transmitters, the Microwave Pico PTT (Platform Transmitter Terminal) from Microwave Telemetry P/L, and the Northstar Solar PTT, Northstar P/L. We deployed these on 13 birds in the Murray-Darling Basin at Fivebough Swamp (34.53°S, 146.44°E) and Barrenbox Swamp (34.13°S, 145.86°E) and on 10 birds in the Lake Eyre Basin at Lake Hope (28.38°S, 139.25°E). We attached PTTs to the back of each bird by a Teflon harness (see Roshier *et al.* 2006). Each transmitter was programmed to run either 7 h ON/17 h OFF (7-h duty cycle) beginning at first light (Northstar solar units) or 10 h ON/24 h OFF (10-h duty cycle; Microwave units). Additionally, to gain an understanding of the timing, duration and speed of long-distance movements, Microwave programmed four units to run continuously for the first 3 months following deployment. We deployed PTT-tagged ducks over a 15-month period between September 2003 and February 2005.

We determined the locations of each duck from location fixes supplied by satellites via the CLS-ARGOS service (Argos 1996). Argos calculated the position of the bird in real-time based on Doppler shift in the frequency received by one or more polar orbiting satellites. We found that the number of fixes per day from any single transmitter could be as many as 25 when running continuously throughout the day and night, but two to four per day was typical for those running on a daily duty cycle of 7 h ON from first activation after sunrise. Argos assigned a nominal location accuracy, location class 3 (< 150 m), 2 (150–350 m), 1 (350–1000 m) or 0 (> 1000 m). We tracked Grey Teal for different periods, from 39 to 879 days, depending on bird survival and the life of the transmitter. Methods for filtering out implausible location fixes are described elsewhere (Roshier *et al.* 2006).

Environmental conditions

We examined the flight paths of all tagged Grey Teal in a geographic information system (GIS), and used for analyses all flights greater than 150 km. Individual Teal did not always fly directly to a new destination, spending from several hours to several days at a location en route to the new destination. Arbitrarily, we considered the bird to have arrived at a new destination once time spent at a location extended beyond 5 days. Using this criterion, the distribution of staging times during and post flight was bimodal. Average staging time during flight was less than 3 days, and staging times post flight were an order of magnitude greater. Once we determined the destination, we performed a search on the Australian Government, Bureau of Meteorology (BOM) website (http://www.bom.gov.au) for the nearest recording weather station. As a result, all weather stations lay within 60 km of the actual location of the tagged Grey Teal. Australia is a broad flat continent with few upland areas to interrupt the movement of weather systems or to alter wind direction and temperature gradients (see Sturman & Tapper 2006). This is particularly so in the region of the study.

We acquired daily rainfall observations at each location for the duration of the study. To identify significant rainfall events, we used a 14-day cumulative total and graphed the results. We used Moderate Resolution Imaging Spectroradiometer (MODIS) satellite imagery to identify flooding events across the Lake Eyre and Murray-Darling basins monthly from September 2003 to March 2006 (31 months). These data have 36 spectral bands ranging from 620 nm to 14 385 nm in the electro-magnetic spectrum. Seven of these bands have a resolution of 250 m or 500 m and we considered only these bands in our study. We used a rule-based classification of landscape features using Normalised Difference Vegetation Indices (NDVI) and the spectral properties of individual MODIS bands (D. Roshier, C. Poynter, T. Edmonds, G. McKenzie, R. Rumbachs, unpubl. data). The NDVI are derived from visible red light and near-infrared radiation (NIR) channels in satellite data and tend to enhance features that have higher NIR reflectance and lower red light reflectance. The index is (NIR – RED)/(NIR + RED) and takes values between –1 and +1. Open water features tend to have negative values (Verdin 1996), bare soil takes values near zero and vegetation takes positive values (McFeeters 1996). Given that healthy vegetation has markedly different NDVI values to open water we added a rule-based classifier that used reflectance in band 6 (Mid-IR) and NDVI to distinguish vegetated wetland areas in addition to areas of open water. A rule-based classifier provides more scope to identify water classes by combining attributes and thresholds in multiple bands. The simplicity of the methodology enabled us to map a wide range of wetland types and for their spatial and temporal dynamics to be determined at broad scales.

We identified the type of the wetland at the destination from 1 : 250 000 topographic maps and Google Earth (http://earth.google.com). We classified (1) streams and lakes as perennial or temporary based on mapped classification, (2) channels and storages associated with irrigation farming as perennial, and (3) ground tanks associated with inhabited homesteads as perennial. We classified all other wetlands as temporary except where we knew from personal experience that a particular wetland was perennial.

Statistical analyses

We categorized Grey Teal movements (1) as those apparently occurring in response to flooding (yes/no) and/or rainfall (< 40, ≥ 40 mm in the previous 14 days) at the destination and origin, and (2) by the type of wetland at the destination (temporary/perennial). We used two-sample *t*-tests to discover the effects of the above factors (rainfall, flooding, wetland type) and the basin of origin (Lake Eyre or Murray-Darling) on flight distance and duration of stay at destination. We used lognormal transformation of the flight data to obtain normality. If transformation did not resolve the non-normality, we used a Mann-Whitney Test on untransformed data. Further, the frequency of flooding and rainfall events at the destination was determined for the periods 0–2 weeks prior to arrival (i.e. conditions associated with migration), and 2–4 weeks prior to arrival. We used a two-tailed Fisher's exact test to compare the frequency of heavy rainfall (≥ 40 mm in the previous 14 days), flooding with low rainfall (< 40 mm in the previous 14 days), and low rainfall for the two periods. All analyses were performed in S-PLUS ver. 7 (Insightful Corp., Seattle, WA, USA).

RESULTS

Long-distance movements

Tagged Grey Teal moved throughout the Murray-Darling Basin in south-eastern Australia and across much of the Lake Eyre Basin in central Australia. Individuals moved up to 978 km between occupied sites, ventured up to 982 km from their point of release, and travelled more than 4300 km in 1 year (Fig. 1). These movements occurred over a period of 31 months up to March 2006, and we tracked one Teal for a total of 879 days.

We identified 32 long-distance (> 150 km) movements that met our criterion for minimally interrupted flight between origin and destination (Table 1). Teal flew up to 1268 km on these flights and three, including the longest, returned to the origin. Teal travelled an average distance of 374.1 ± 315.2 km (mean ± sd) in the agricultural landscapes of the Murray-Darling Basin and 394.7 ± 256.4 km in the desert landscapes of the Lake Eyre Basin.

Thirteen of the 32 flights coincided with heavy rainfall (> 40 mm in the previous 14 days) at the destination (n = 8) or the flooding (n = 8) associated with it. Flights to areas of recent flooding occurred over distances up to 1051 km. In an additional 11 cases there had been some rain (up to 29.6 mm in the previous 14 days) at the destination. On only three flights did we record no flooding or rain in the previous 14 days at the destination (in another four cases no rainfall data were available).

Individual Grey Teal stayed from several days to more than 1 year at the new destination (Table 1).

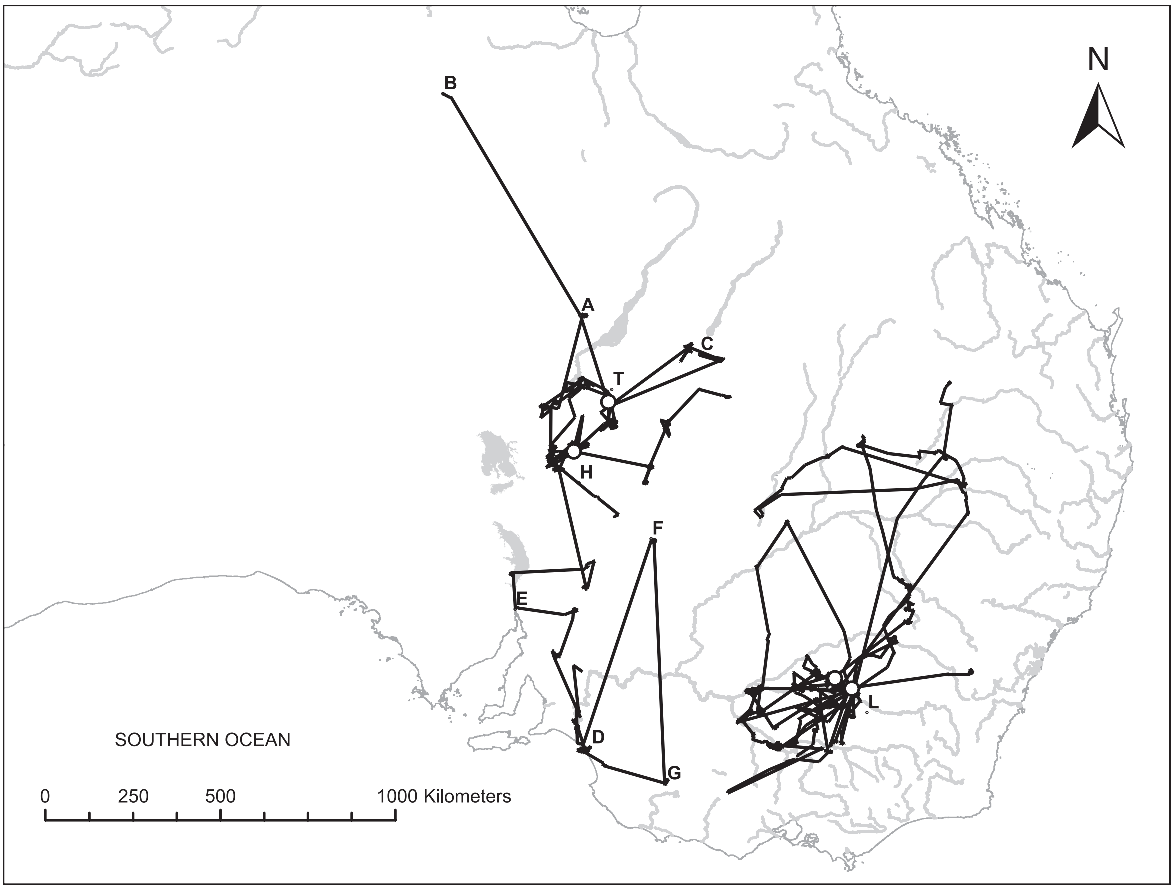

Figure 1. Movement paths of 23 Grey Teal released at Fivebough Swamp (34.53°S, 146.44°E) near Leeton (L) in the Murray-Darling Basin of southern Australia on 2 and 3 November 2004 and at Lake Hope (H: 28.38°S, 139.25°E) and Lake Toontoowaranie (T: 27.10°S, 140.18°E) in the Lake Eyre Basin. Letters indicate geographic locations referred to in text: A, Eyre Creek; B, Barkly Tableland; C, Windorah; D, Coorong; E, Port Augusta; F, Fowlers Gap; and G, Lake Miga. Grey lines indicate major rivers and streams.

Table 1a. Long-distance flights of Grey Teal released in the Murray-Darling Basin. Flights in bold designate those for which there was 40 mm of rainfall in the previous 2 weeks or flooding at the destination.

Bird ID	Description of movement	Date	Distance (km)	Duration (days)	Rainfall at origin (mm)	Rainfall at destination (mm)	Flooding at destination	Wetland type at destination	Duration at destination (days)
40871	Permanent swamp to sewerage treatment works	17/11/2003	286	0.9	0.2	0.0	no	Perennial	17
	Irrigation channels to permanent swamp	28/01/2004	241	7.9	0.0	0.0	no	Perennial	55
40874	Permanent swamp to irrigated farmland	06/09/2003	170	1.8	37.0	13.0	no	Perennial	15
	Irrigated farmland to permanent swamp	10/10/2003	155	7.8	28.4	3.8	no	Perennial	11
	Permanent swamp to perennial watercourse	29/10/2003	153	11.1	7.6	no data	no	Perennial	6
	Perennial watercourse to permanent swamp	29/05/2004	**160**	7.0	no data	40.0	no	Perennial	10
	Permanent swamp to temporary swamp	10/12/2004	**191**	8.0	14.0	110.4	no	Temporary	31
45882	Permanent swamp to watercourse	15/06/2004	**239**	1.0	16.2	40.2	no	Temporary	186
45885	Permanent swamp to watercourse	09/03/2004	317	3.0	0.0	13.6	no	Temporary	73
52089	Permanent swamp to irrigated farmland	13/12/2004	281	2.2	15.0	29.6	no	Perennial	109
52090	Irrigated farmland to irrigated farmland and return	23/11/2004	324	2.0	18.0	18.0	no	Perennial	16
	Irrigated farmland to permanent wetland	11/12/2004	**189**	0.6	38.8	76.4	yes	Perennial	393
52091	Irrigated farmland to water storage	27/02/2005	**1051**	13.5	2.2	2.2	yes	Perennial	7
52092	Permanent swamp to irrigated farmland	06/11/2004	397	2.3	21.0	22.1	no	Temporary	32
	Irrigated farmland to temporary wetland	10/12/2004	514	3.4	49.6	0.4	no	Temporary	24
	Temporary wetland to temporary wetland	06/01/2005	**423**	4.1	1.2	3.4	yes	Temporary	15
	Temporary wetland to temporary wetland and return	25/01/2005	**1268***	4.5+	53.6	51.0	yes	Temporary	22

*Transmitter switched duty-cycle after 4.5 days when the bird had travelled 861 km. Next location 1 week later was at origin.

Table 1b. Long-distance flights of Grey Teal released in the Lake Eyre Basin. Flights in bold designate those for which there was 40 mm of rainfall in the previous 2 weeks or flooding at the destination.

Bird ID	Description of movement	Date	Distance (km)	Duration (days)	Rainfall at origin (mm)	Rainfall at destination (mm)	Flooding at destination	Wetland type at destination	Duration at destination (days)
40872-1	Semi-permanent lake to farm ground tank	21/11/2003	255	1.7	11.6	6.2	no	Temporary	10
	Temporary watercourse to temporary watercourse	30/04/2004	202	2.9	no data	no data	no	Temporary	12
40872-2	Temporary wetland to temporary watercourse	24/03/2005	978	1.8	no data	no data	no	Temporary	Died at dest.
40873	Temporary wetland to farm ground tank	12/08/2004	343	1.0	0.0	11.4	no	Perennial	49
	Farm ground tank to watercourse	08/11/2004	182	0.9	14.4	no data	no	Temporary	29
	Watercourse to farm ground tank	08/12/2004	**443**	8.7	no data	46.0	no	Perennial	81
	Permanent wetland to temporary watercourse	14/07/2005	**612**	4.0	22.0	54.2	no	Temporary	29
	Temporary watercourse permanent wetland	16/08/2005	921	10.0	2.0	17.8	no	Perennial	7
41421	Temporary wetland to permanent waterhole	24/01/2004	175	2.5	0.0	15.0	no	Perennial	7
	Permanent waterhole to temporary watercourse	02/02/2005	**304**	1.3	0.0	0.0	yes	Temporary	79
41423	Temporary wetland to temporary wetland and return	01/11/2003	215	5.3	0.0	0.0	no	Temporary	14
	Temporary wetland permanent waterhole	10/12/2003	347	16.6	0.0	0.0	no data	Perennial	Died at dest.
41422	Perennial watercourse to temporary watercourse	15/01/2004	**432**	3.9	0.0	106.3	yes	Temporary	10
	Temporary watercourse to temporary watercourse	29/01/2004	**161**	2.8	78.4	7.6	yes	Temporary	43
	Temporary watercourse to perennial watercourse	15/03/2004	**350**	2.8	3.6	0.0	yes	Perennial	50

The average number of days spent at the new destination was 60.1 ± 97.5 (mean ± sd) in the agricultural landscapes of the Murray-Darling Basin and 32.3 ± 26.3 in the desert landscapes of the Lake Eyre Basin.

Analyses of factors associated with long-distance flights showed that there was no relationship between flight distance and (1) flooding (yes/no), (2) rainfall at the origin (< 40, ≥ 40 mm), (3) rainfall at the destination (< 40, ≥ 40 mm), (4) type of wetland at the destination (temporary/perennial), or (5) drainage basin of origin. The same was true of duration of stay at the destination, except for rainfall, with which duration of stay increased from a mean of 29.1 days to 95.3 days when rainfall was ≥ 40 mm in previous 14 days ($t = -2.08$, df = 24, $P < 0.05$).

Timing and weather conditions

The frequency of heavy rainfall events or flooding at the destination was significantly greater in the 2 weeks immediately prior to migration than in the period 2–4 weeks prior (48% of flights versus 19%, $P = 0.02$, Fisher's exact test). The timing of movement in relation to rainfall and/or flooding was in some instances precise, with Teal arriving within hours of a rainfall event or the arrival of floodwaters. For example, heavy rainfall in the upper catchment of Cooper Creek in January 2004 resulted in moderate flooding along hundreds of kilometres of the Cooper Creek floodplain. Floodwaters arrived near Windorah (26.02°S, 143.10°E) in southwest Queensland on 17 January 2004 following rains that commenced on 12 January 2004 and were at their heaviest locally in the 24 h after 09:00 h on 15 January when 62.2 mm fell. A tagged Grey Teal, #41422, left a permanent waterhole on Cooper Creek 360 km to the southwest near Innamincka sometime after 19:00 h on 15 January and arrived to meet the floodwaters at Windorah sometime before 07:42 h on 18 January (Fig. 2). Somewhat surprisingly, this bird returned to near its original location on Cooper Creek on

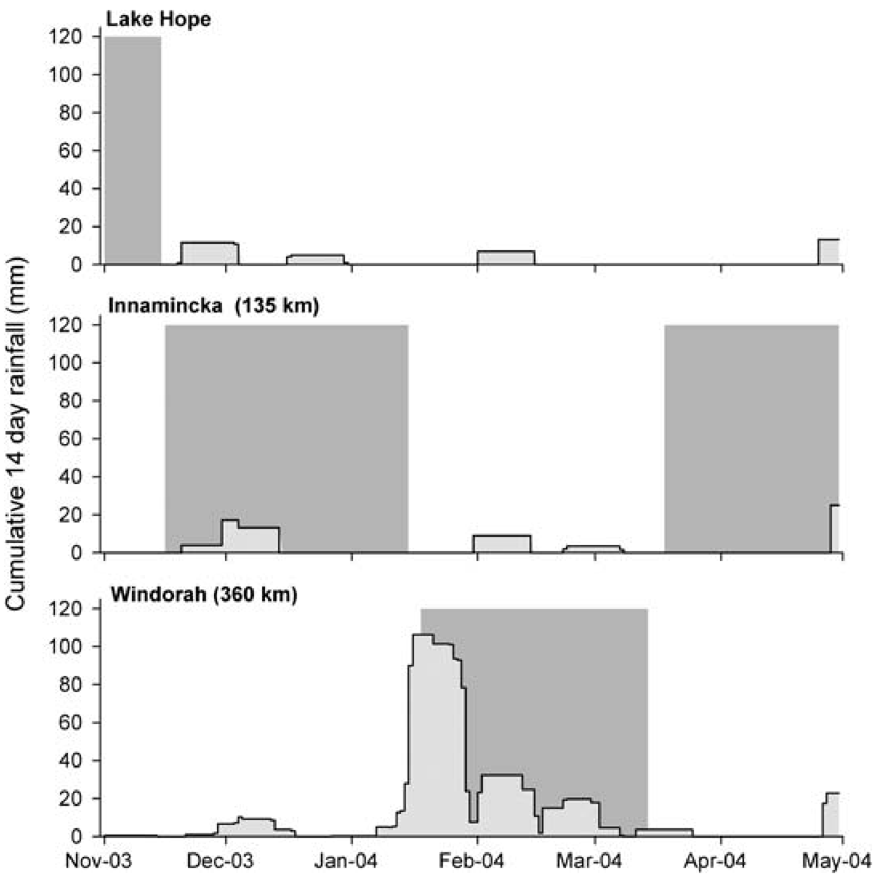

Figure 2. Period of occupancy (grey bar) during the course of the study of #41422 at sites along its movement path. Hatched bar shows cumulative rainfall in the previous 14 days. Distance in brackets indicates path length from previous occupied site.

18 March 2004 about 6 days after the floodwaters reached that location and approximately 1 day after the flood peak (data source Bureau of Meteorology, Melbourne). In all cases for which data are available the bird arrived at its destination between 1 and 13 days (7.6 ± 4.2 days, mean ± sd, $n = 7$) after the peak of the rainfall event defined by the 24-h period during which most rain fell.

The Grey Teal tracked the longest (#40873) moved from the temporary wetlands of the Lake Eyre Basin to the coastal wetlands of the Coorong (35.87°S, 139.36°E) over 900 km to the south via semi-arid regions with little surface water, estuarine habitats in the Spencer Gulf near Port Augusta (32.44°S, 137.76°E), and farmland in the settled regions of South Australia. The cues for movement were most obvious when the bird moved to or from the arid interior, in response to rainfall events (Fig. 3). This included a 612-km flight from the permanent waters of the Coorong to a temporary watercourse near Fowlers Gap (30.64°S, 141.26°E) in western New South Wales following heavy rain. After 29 days at this location, #40873 returned to the permanent wetlands of Coorong over the next 10 days along a 921-km flight path via Lake Miga (36.93°S, 141.64°E) in western Victoria.

Three flights were from origin to origin without staying at any intervening site long enough for that site to qualify as a destination. Two of these flights occurred in response to no obvious environmental cue. In the third instance the Teal (#52092) left an area that had experienced heavy rain and flooding to move approximately 600 km into a region of the arid interior that had experienced no rainfall and then returned immediately to the origin. The rate of movement during the early phase of this flight was rapid, with the Teal travelling 502 km in the first 6.6 h, with an average groundspeed of 99.9 km/h for half of that period. All extended legs of this 1268-km flight were undertaken at night.

DISCUSSION

Most Grey Teal at some stage during this study apparently responded to distant environmental cues such as rainfall and flooding. Intuitively, we know that Grey Teal must be able to find distant wetlands or they will perish on a mostly arid continent. More surprising was that some undertook long flights over hundreds of kilometres into regions that at the time had little surface water, settling on small persistent water sources in regions that rarely had significant areas of surface water. These apparent prospecting flights may be analogous to 'ranging behaviour' (Dingle 1996, 2006). Dingle describes this behaviour as facultative, and movement ceases when the resources being sought are encountered. This conforms to our general understanding of what constitutes nomadic movement behaviour. Counter to the idea that ranging behaviour is a suitable description for all long-distance flights of Grey Teal are the movements of individuals across regions of diverse and numerous wetland resources to settle on distant wetlands, bypassing many wetlands encountered along the way and continuing in response to no apparent environment cue. For example, Teal #40872-1 flew 286 km overnight across extensive areas of irrigated rice crops to settle on a sewerage treatment works for 17 days.

Analyses of the complete movement paths of Grey Teal in this study showed that movement is a complex behavioural strategy across all scales that varies between individuals and is not a simple response to patterns (seasonal or otherwise) of resource distribution (Roshier *et al.* 2008). From the point of view of understanding environmental cues it is worth noting that some movement paths were scale-variant (i.e. moving with different levels of tortuosity at different spatial scales). This suggests that movement is prescient (i.e. based upon prior knowledge or predictive ability) even at broad scales – as in long-distance seasonal migrants.

In a stochastic environment there must be other than endogenous controls of movement and migration cued to the seasons. In this study, 13 of the 32 flights coincided with identifiable environmental events such as rainfall and flooding at the destination site (Table 1). This suggests that these long-distance flights occurred with prior knowledge of wetland conditions, such as long flights to intercept floodwaters long after the weather signal that produced the flooding had dissipated. In five of the eight instances when Teal moved to recently flooded areas, little or no rainfall occurred during the previous 14 days. Nonetheless, most of the long-distance flights in this study took place without any obvious cue indicating newly available resources at the destination site – suggesting that something other than a weather or wetland related cue initiated the movement response.

Species that interact with temporary resources at broad scales may use periods of high resource abundance to locate particular resources for future use – the exploration hypothesis (Bell 1991). The patterns of movement of Grey Teal observed in this

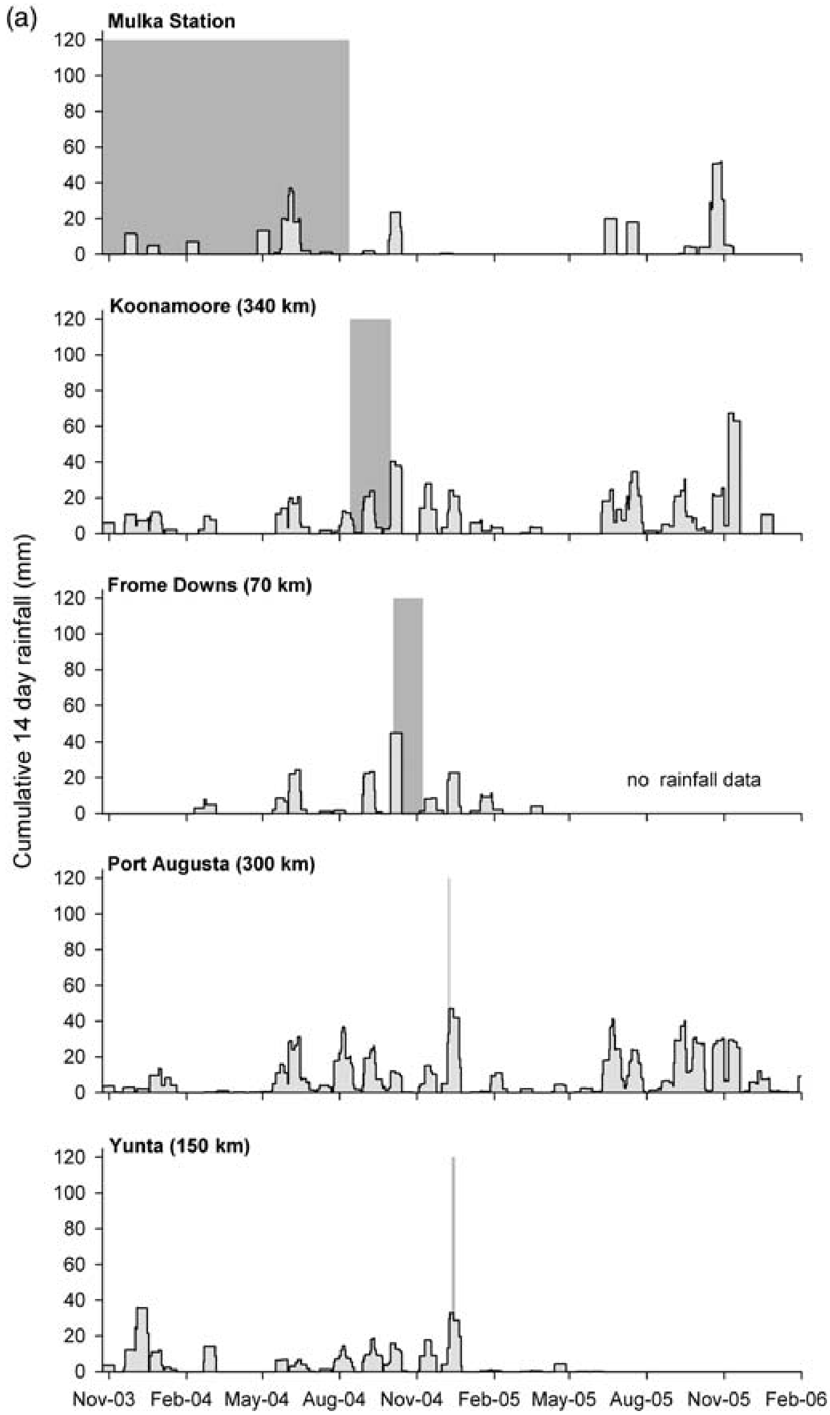

Figure 3. Period of occupancy (grey bar) during the course of the study of #40873 at sites along its movement path. Hatched bar shows cumulative rainfall in the previous 14 days. Distance in brackets indicates path length from previous occupied site.

study are in part consistent with the exploration hypothesis in that individual Teal undertook long flights following periods of extended rainfall or flooding at the point of origin (Table 1). Spatial memory (Benhamou & Poucet 1995; Benhamou 1997) is known to be highly developed in some bird species (Bingman & Able 2002, Benhamou *et al.* 2003, Lipp *et al.* 2004) and is one of a number of

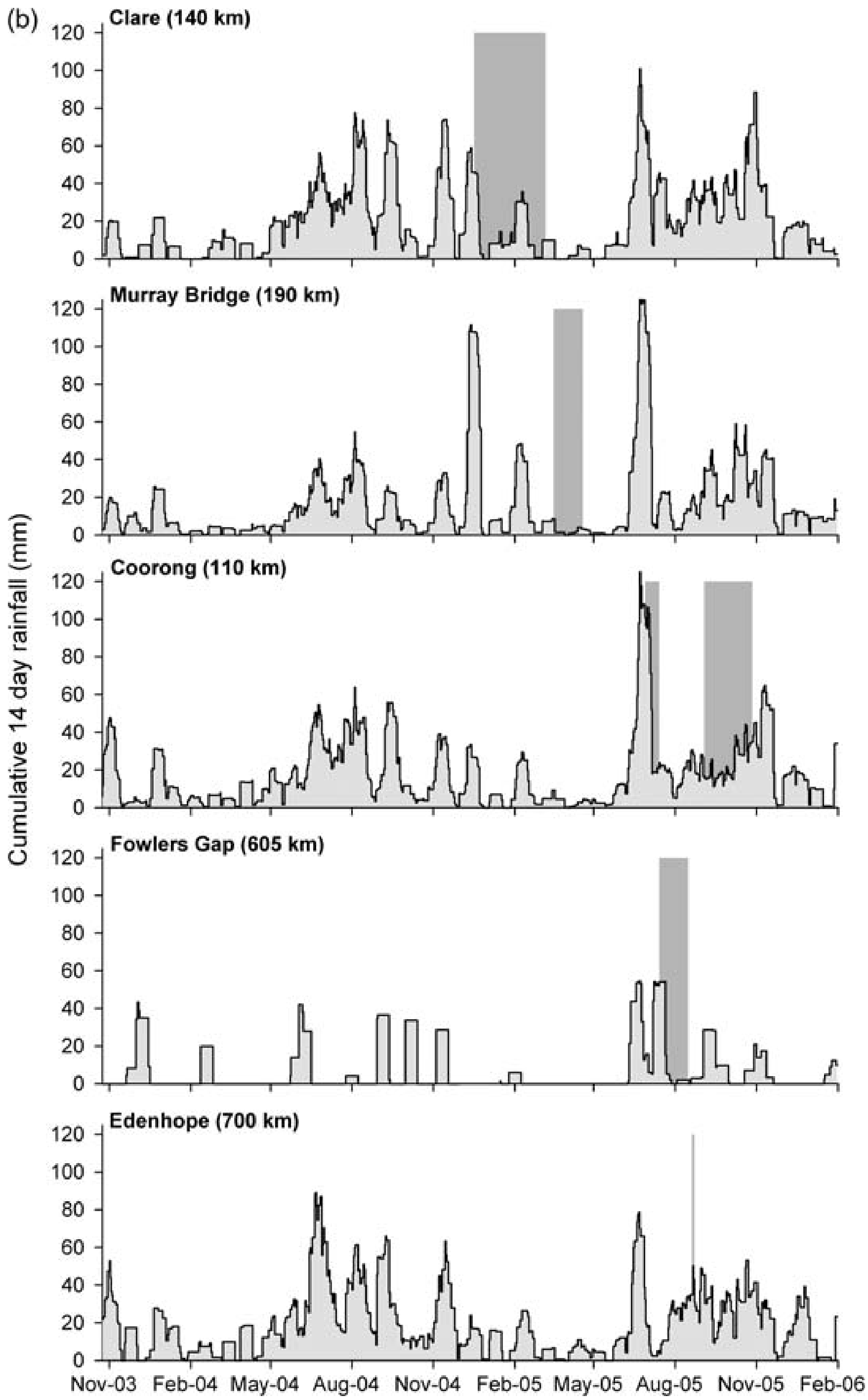

Figure 3. *Continued*

orientation and navigation processes used to return to known resources. The longest observed flight in this study covered more than 1200 km across a region with little surface water before returning to an area of recent flooding a few days later (Table 1). This flight was impressive as a feat of navigation as this Teal, #52092, returned to the same group of wetlands previously occupied. Another wetland-dependent nomadic species, the Snail Kite *Rostrhamus sociabilis*, ranged further during periods of high resource abundance (Bennetts & Kitchens 2000). The explanation is that knowledge of the distribution of resources at broad scales can be gained during periods of high resource availability at reduced energetic cost or risk of predation compared to periods of low resource availability. The authors concluded that Snail Kites altered the nature and extent of movement in response to changes in patterns of resource distribution. As resources decline there is probably greater fitness and likelihood of survival for those individuals whose movements are prescient and who move directly to known resources.

If Grey Teal are the same as other *Anas* ssp., the observed distances moved in the current study suggest that the long-distance movements have high energy costs (Norberg 1996). In an environment where the population dynamics of prey species are pulsed (Timms 1998, Puckridge *et al.* 1998, Sheldon *et al.* 2002, Bunn *et al.* 2003) and flood events infrequent (Roshier *et al.* 2001a, 2001b) the acquisition of additional energy stores for breeding or escape is likely to be time critical, just as it is for long-distance seasonal migrants (Petrie & Rogers 2004). Waterbirds using temporary wetland habitats in arid environments for breeding are time-constrained as evaporation and prey dynamics combine to limit the time for which prey items are available to feed young. Storage of fat prior to arrival at breeding sites reduces 'reproductive uncertainty' associated with utilizing time-limited resources (Petrie & Rogers 2004). Thus, some so-called nomadic species respond to variable patterns of resource availability using the same behavioural strategies as long-distance seasonal migrants in temperate landscapes.

In conclusion, besides sharing ultimate factors (e.g. Smith 1970), the proximate factors driving long-distance movements of waterfowl in Australia need not be very different from those of their temperate counterparts. For nomadic species, knowledge of the spatial distribution of resources, such as food resources, at broad scales increases life-time fitness and survival (Bennetts & Kitchens 2000), as it does in long-distance seasonal migrants (Mettke-Hofmann & Greenberg 2005). Endogenous control might play a key role in northern-temperate migrants, but both groups interact with available resources at broad scales and can have similar physiological responses to resource constraints. Waterfowl movement patterns in Australia may simply be the expression of one part of a broader movement strategy that is keyed to the availability of resources and shared by related species in more seasonal and predictable environs.

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