Use of radio telemetry in studies of shorebirds: past contributions and future directions

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Warnock, N. & Takekawa, J.Y. 2003. Use of radio telemetry in studies of shorebirds: past contributions and future directions. *Wader Study Group Bull.* 100: 138–150.

The use of radio telemetry in wader studies has grown exponentially in the past decade, and more than 40 species from four different families have been radio-marked. We summarize these studies and find that nearly all of them have used Very High Frequency radio transmitters to study individuals for periods from a few days to a few months. In the past five years, there has been tremendous growth in studies of larger birds with satellite telemetry, but currently there is only one published satellite telemetry study of a wader, the Eastern Curlew. We discuss technical details including the various methods that have been used to affix transmitters to waders. Telemetry studies of waders have made significant contributions to understanding space use, distribution, migration, survival, and population size. A recent, January 2003, workshop on "The use and future of automated radio-tracking systems in bird migration studies", indicated that these have the capacity to gather tremendous amounts of data pertaining to wader ecology in relatively short amounts of time. Through the innovative use of telemetry, it is likely that new information on wader ecology that has previously been unattainable will soon emerge.

INTRODUCTION

Radio telemetry is a powerful tool that has led to tremendous advances in many areas of wildlife ecology. Studies of radio-marked individuals have provided detailed information on movements and distribution of fast-moving or secretive species that are difficult to observe without such technology. Radio telemetry was first used to study waders (syn. with shorebirds) in the late 1960s. It appears as if, in 1967, the American Woodcock (scientific names of waders listed in Table 1) was the first wader radio-marked for field studies (R.B. Owen pers. comm., Schemnitz & Owen 1969, Marshall *et al.* 1971, Ramakka 1971, 1972, but see Tuck 1972). Despite early pioneering efforts such as these on upland game species, few researchers studying other wader populations applied radio telemetry techniques until the 1980s (Warnock & Warnock 1993). However, the use of radio telemetry in wader studies has grown exponentially in the past decade. More than 40 species of waders representing four different families (Scolopacidae, Haematopodidae, Recurvirostridae, and Charadriidae) have now been radio-marked (Table 1).

The increasing use of radio telemetry for wildlife research has followed recent developments in miniaturization of consumer electronics. Smaller electronic components, circuit boards, and power sources have resulted in development of transmitters of <0.4 g, suitable for marking even the smallest waders and their chicks. Small solar panels also have provided an alternative power source to batteries in limited applications with larger transmitters. At the same time, other advances in technology such as deployment of satellite location systems capable of tracking platforms from space present even greater future opportunities for use in wader research. In this paper, we review past efforts, current use, and future potential of telemetry in studies of wader ecology. We discuss transmitters, attachment techniques, and applications in several fields of wader ecology.

TYPES OF TRANSMITTERS

Nearly all telemetry applications for waders have used Very High Frequency (VHF) radio transmitters and receiving systems to study individual birds for periods of a few days to a few months. These transmitters typically transmit continuously at pulse rates of 0.5–1.5 times per second at frequencies between 140 and 180 megahertz (MHz) and occasionally into the 200 MHz range (Kenward 1987, Samuel & Fuller 1996). These tags are generally 1–2 cm long and weigh <4 g.

In the past five years, there has been tremendous growth in studies of larger birds such as waterfowl and seabirds with satellite telemetry. Satellite transmitters or platform transmitter terminals (PTTs) send 20- to 32-bit digital signals that are collected and processed by the Argos (Argos, Inc.) receiving system on NOAA polar-orbiting weather satellites. PTTs transmit at 401.65 MHz during a fixed interval (60–65 s) to the satellites orbiting 160 km above the surface. The signal is detected during 5–15 minute satellite overpasses that occur every 1–2 hours, and the location of the transmitter is calculated by the change in frequency or Doppler shift during the overpass (Kenward 1987, Samuel & Fuller 1996). Bird-borne PTTs are programmed to transmit for a few hours every 1–7 days, providing one or more locations with a rough accuracy of 1–10 km.

Reviews have suggested limiting use of radio transmitters to 3–5% of a bird's mass (Caccamise & Hedin 1985, Take-

Table 1. Published wader telemetry studies by species and year of publication. Species names and order after Del Hoyo (1996).

Species	Author(s)	Season	Description	Location
Scolopacidae				
Eurasian Woodcock *Scolopax rusticola*				
	Hirons & Owen 1982	Breeding	radio effect, breeding behaviour	United Kingdom
American Woodcock *Scolopax minor*				
	Schemnitz & Owen 1969	Breeding	pilot breeding study	Maine
	Marshall *et al.* 1971.		review of telemetry studies	Minnesota
	Ramakka 1971	Breeding	behaviour of males	Maine
	Ramakka 1972	Breeding	behaviour of males	Maine
	Dunford & Owen 1973	Breeding	behaviour of immatures	Maine
	Wenstrom 1973	Breeding	habitat use and behaviour of females	Minnesota
	Owen & Morgan 1975	Breeding	behaviour of adults	Maine
	Coon *et al.* 1976a	Migratory	fall migration of one bird	Pennsylvania
	Coon *et al.* 1976b	Migratory	female fall migration	Pennsylvania
	Horton & Causey 1979	Breeding	movements and habitat use	Alabama
	Storm & Wakeley 1981	Breeding	habitat selection of males	Pennsylvania
	Gregg 1984	Breeding	population ecology	Wisconsin
	Horton & Causey 1984	Breeding	brood abandonment by females	Alabama
	Hudgins *et al.* 1985		movements and habitat use	Pennsylvania
	Derleth & Sepik 1990	Breeding and non-breeding	survival	Maine
	McAuley *et al.* 1993a		review of telemetry techniques	
	McAuley *et al.* 1993b	Breeding	behaviour	
	Krementz *et al.* 1994	Non-breeding	survival	Atlantic Coast, USA
	Krementz & Pendleton 1994	Non-breeding	diurnal habitat use	Atlantic Coast, USA
	Lang 1994	Migratory	migration	Pennsylvania
	Krementz *et al.* 1995	Non-breeding	nocturnal habitat use	Georgia and Virginia
	Longcore *et al.* 1996	Breeding	survival	Maine
	Krementz & Berdeen 1997	Non-breeding	survival	Georgia
	Berdeen & Krementz 1998	Non-breeding	nocturnal habitat use	Georgia
	Pace 2000	Non-breeding	survival	Louisiana
Latham's Snipe *Gallinago hardwickii*				
	Todd 2000	Non-breeding	feeding ecology	NSW, Australia
Great Snipe *Gallinago media*				
	Kålås *et al.* 1989	Breeding	effects of transmitters	Norway
	Höglund & Robertson 1990	Breeding	home range and behaviour	Sweden
Common Snipe *Gallinago gallinago*				
	Tuck 1972	Breeding	nesting behaviour	Canada
	Hoodless *et al.* 2000	Non-breeding	habitat use and diet	England
Jack Snipe *Lymnocryptes minimus*				
	Pedersen 1995	Non-breeding	habitat use and movements	Denmark

Table 1 cont. Published wader telemetry studies by species and year of publication. Species names and order after Del Hoyo (1996).

Species	Author(s)	Season	Description	Location
Bar-tailed Godwit *Limosa lapponica*				
	Exo *et al.* 1996	Non-breeding	transmitter test	Germany
	Rohweder 1999	Non-breeding	transmitter attachment test	NSW, Australia
	Green *et al.* 2002	Migratory	connectivity	Eastern Atlantic Flyway
Marbled Godwit *Limosa fedoa*				
	Gabbard *et al.* 2001	Non-breeding	home range	Florida
Whimbrel *Numenius phaeopus*				
	McNeil & Rompré 1995	Non-breeding	diurnal and nocturnal behaviour	Venezuela
	Rohweder 1999	Non-breeding	transmitter attachment test	NSW, Australia
Bristle-thighed Curlew *Numenius tahitiensis*				
	Gill *et al.* 1991	Breeding	habitat use and behaviour	Alaska
Eurasian Curlew *Numenius arquata*				
	Robson 1998	Breeding	chick movements	United Kingdom
	Grant 2002	Breeding	weight gain and survival	United Kingdom
Long-billed Curlew *Numenius americanus*				
	Redmond 1984	Breeding	chick behaviour	Idaho
	Redmond & Jenni 1986	Breeding	chick behaviour	Idaho
	Gabbard *et al.* 2001	Non-breeding	home range	Florida
Eastern Curlew *Numenius madagascariensis*				
	Driscoll & Minton 1999	Migratory	connectivity	Eastern Pacific Flyway
	Minton & Driscoll 1999	Migratory	connectivity	Eastern Pacific Flyway
	Rohweder 1999	Non-breeding	transmitter attachment test	NSW, Australia
	Driscoll & Ueta 2002	Migratory	connectivity	Eastern Pacific Flyway
Upland Sandpiper *Bertramia longicauda*				
	Ailes & Toepfer 1977	Breeding	home range and daily movments	Wisconsin
Common Redshank *Tringa totanus*				
	Burton 2000	Non-breeding	site-fidelity and survival	Wales
Green Sandpiper *Tringa ochropus*				
	Smith 1987	Non-breeding	nocturnal behaviour	United Kingdom
	Smith *et al.* 1999	Non-breeding	diurnal and nocturnal movements	United Kingdom
Terek Sandpiper *Tringa cinerea*				
	Rohweder 1999	Non-breeding	transmitter attachment test	NSW, Australia
Grey-tailed Tattler *Tringa brevipes*				
	Rohweder 1999	Non-breeding	transmitter attachment test	NSW, Australia
Willet *Catoptrophorus semipalmatus*				
	McNeil & Rompré 1995	Non-breeding	diurnal and nocturnal behaviour	Venezuela

Table 1 cont. Published wader telemetry studies by species and year of publication. Species names and order after Del Hoyo (1996).

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	Rompré & McNeil 1996	Non-breeding	diurnal and nocturnal habitat use	Venezuela
	Gabbard *et al.* 2001	Non-breeding	home range	Florida
	Haig *et al.* 2002	Breeding	space use	Great Basin, USA
Ruddy Turnstone ***Arenaria interpres***				
	Smart & Gill 2002	Non-breeding	habitat use	United Kingdom
	Smart & Gill in press	Non-breeding	habitat use	United Kingdom
Short-billed Dowitcher ***Limnodromus griseus***				
	Warnock *et al.* 2001	Migratory	stopover ecology and connectivity	Western Pacific Flyway
Long-billed Dowitcher ***Limnodromus scolopaceus***				
	Warnock *et al.* 2001	Migratory	stopover ecology and connectivity	Western Pacific Flyway
	Takekawa *et al.* 2002	Non-breeding	home range and movements	California
	Warnock *et al.* 2002	Migratory	stopover ecology and connectivity	Western Pacific Flyway
Surfbird ***Aphriza virgata***				
	Gill *et al.* 1999	Breeding	habitat use and movements	Alaska
Great Knot ***Calidris tenuirostris***				
	Battley 2000	Non-breeding	habitat use	Western, Australia
	Battley 2002	Migratory	departure dates	Western, Australia
Red Knot ***Calidris canutus***				
	Tulp *et al.* 1998	Breeding	movements	Russia
	Baker *et al.* 1999	Migratory	connectivity	Argentina and Brazil
	Van Gils & Piersma 1999	Migratory	diurnal and nocturnal movements	The Netherlands
	Nebel *et al.* 2000	Migratory	stopover ecology	The Netherlands
	Niles *et al.* 2001	Migratory	connectivity	Eastern Atlantic Flyway
	Sitters *et al.* 2001	Non-breeding	diurnal and nocturnal habitat use	Argentina
Sanderling ***Calidris alba***				
	Evans 1996	Migratory	connectivity	England, Iceland
	Rohweder 1999	Non-breeding	transmitter attachment test	NSW, Australia
Semipalmated Sandpiper ***Calidris pusilla***				
	Skagen & Knopf 1994	Migratory	stopover ecology	Central Flyway, USA
	Cresswell *et al.* in press	Breeding	incubation behaviour	Alaska
Western Sandpiper ***Calidris mauri***				
	Warnock & Warnock 1993		attachment of transmitters	California
	Warnock & Takekawa 1995	Non-breeding	habitat use	California
	Butler *et al.* 1996	Migratory	connectivity	Western Pacific Flyway
	Iverson *et al.* 1996	Migratory	connectivity and stopover ecology	Western Pacific Flyway
	Warnock & Takekawa 1996	Non-breeding	site fidelity and movements	California
	Warnock & Bishop 1996	Migratory	stopover ecology	Western Pacific Flyway
	Bishop & Warnock 1998	Migratory	connectivity	Western Pacific Flyway

Table 1 cont. Published wader telemetry studies by species and year of publication. Species names and order after Del Hoyo (1996).

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	Sanzenbacher *et al.* 2000		harness attachment	USA
	Warnock *et al.* 2002	Migratory	stopover ecology and connectivity	Western Pacific Flyway
Rufous-necked Stint ***Calidris ruficollis***				
	Rohweder 1999	Non-breeding	transmitter attachment test	NSW, Australia
White-rumped Sandpiper ***Calidris fuscicollis***				
	Skagen & Knopf 1994	Migratory	stopover ecology	Central Flyway, USA
Pectoral Sandpiper ***Calidris melanotos***				
	Farmer & Parent 1997	Migratory	stopover ecology	Central Flyway, USA
	Farmer & Wiens 1999	Migratory	modelling migration	Central Flyway, USA
Purple Sandpiper ***Calidris maritima***				
	Cresswell & Summers 1988	Breeding	behaviour	Norway
	Summers 1994	Non-breeding	diurnal and nocturnal behaviour	Scotland
Rock Sandpiper ***Calidris ptilocnemis***				
Dunlin ***Calidris alpina***				
	Warnock & Warnock 1993	Non-breeding	attachment of transmitters	California
	Warnock *et al.* 1995	Non-breeding	local movements	California
	Warnock 1996	Non-breeding	local movements and habitat use	California
	Sanzenbacher *et al.* 2000	Non-breeding	harness attachment	USA
	Shepherd 2001	Non-breeding	space use, habitat preferences	Canada
	Warnock *et al.* 2001	Migratory	stopover ecology, connectivity	Western Pacific Flyway
	Sanzenbacher & Haig 2002a	Non-breeding	movements	Oregon
Curlew Sandpiper ***Calidris ferruginea***				
	Rohweder 1999	Non-breeding	transmitter attachment test	NSW, Australia
Buff-breasted Sandpiper ***Tryngites subruficollis***				
	Lanctot 1994	Breeding	movements and survival of juveniles	Alaska
	Lanctot *et al.* 1997	Breeding	lekking behaviour	Alaska
	Lanctot *et al.* 1998	Breeding	male breeding behaviour	Alaska
Wilson's Phalarope ***Phalaropus tricolor***				
	Colwell & Oring 1988	Breeding	female behaviour	Saskatchewan
Haematopodidae				
Eurasian Oystercatcher ***Haematopus ostralegus***				
	Exo 1992	Breeding	time activity, transmitter function	Germany
	Exo *et al.* 1992	Breeding	time activity, transmitter function	Germany
	Exo 1993	Breeding	time activity, transmitter function	Germany
	Exo & Scheiffarth 1993	Breeding	time activity, transmitter function	Germany
	Sitters 2000	Non-breedng	nocturnal behaviour	England

Table 1 cont. Published wader telemetry studies by species and year of publication. Species names and order after Del Hoyo (1996).

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American Oystercatcher				
	Gabbard *et al.* 2001	Non-breeding	home range	Florida
Recurvirostridae				
Black-winged Stilt *Himantopus himantopus*				
	Hickey 2002	Breeding	home range	California
American Avocet *Recurvirostra americana*				
	Plissner *et al.* 1999	Migratory	connectivity and movements	Great Basin, USA
	Plissner *et al.* 2000a	Migratory	post-breeding movements	Great Basin, USA
Charadriidae				
Eurasian Golden-Plover *Pluvialis apricaria*				
	Byrkjedal 1985	Breeding	time-activity budget	Norway
	Yalden 1991	Breeding	chick movements	United Kingdom
	Ketzenberg & Exo 1996	Migratory	habitat choice	Germany
	Whittingham 1996	Breeding	feeding behaviour	United Kingdom
	Ketzenberg & Exo 1997	Migratory	diurnal and nocturnal movements	Germany
	Whittingham *et al.* 1999a	Breeding	nocturnal chick movements	United Kingdom
	Whittingham *et al.* 1999b	Breeding	chick habitat use	United Kingdom
	Whittingham *et al.* 2000	Breeding	time budgets and feeding	United Kingdom
Pacific Golden-Plover *Pluvialis fulva*				
	Johnson *et al.* 1997	Migratory	connectivity and survival	Hawaii and Alaska
	Rohweder 1999	Non-breeding	transmitter attachment test	NSW, Australia
	Johnson *et al.* 2001	Migratory	connectivity and survival	Hawaii and Alaska
Grey Plover *Pluvialis squatarola*				
	Dugan 1981	Non-breeding	nocturnal feeding	England
	Wood 1986	Non-breeding	diurnal and nocturnal territoriality	England
	Gabbard *et al.* 2001	Non-breeding	home range	Florida
Wilson's Plover *Charadrius wilsonia*				
	Thibault & McNeil 1995	Non-breeding	diurnal and nocturnal incubation	Venezuela
Killdeer *Charadrius vociferus*				
	Warnock & Oring 1996	Breeding	nocturnal incubation	California
	Powers 1998	Breeding	home range and space use	California
	Plissner *et al.* 2000b	Breeding	home range and space use	California
	Sanzenbacher *et al.* 2000	Non-breeding	harness attachment	USA
	Sanzenbacher & Haig 2002b	Non-breeding	fidelity and movements	Oregon
Piping Plover *Charadrius melodus*				
	Drake *et al.* 2001	Non-breeding	movements, habitat use, and survival	Texas

Table 1 cont. Published wader telemetry studies by species and year of publication. Species names and order after Del Hoyo (1996).

Species	Author(s)	Season	Description	Location
Kentish Plover *Charadrius alexandrinus*				
	Hill & Talent 1990	Breeding	effect of transmitter	Oklahoma
	Kosztolányi & Székely 2002	Breeding	transponders and incubation	Turkey
Double-banded Plover *Charadrius bicinctus*				
	Rohweder 1999	Non-breeding	transmitter attachment test	NSW, Australia
	Keedwell 2001	Breeding	chick mortality	New Zealand
	Rohweder & Lewis 2001	Non-breeding?	diurnal and nocturnal habitat use	NSW, Australia
Mountain Plover *Charadrius montanus*				
	Miller & Knopf 1993	Breeding	growth and fledgling survival	Colorado
	Knopf & Rupert 1995	Non-breeding	habitat use and movements	California
	Knopf & Rupert 1996	Breeding	behaviour and movements	Colorado

kawa & Orthmeyer 2001). Currently, the smallest PPTs weigh 15–20 g, which limits their use to birds at least 400–600 g. So far, there is only one published study of a wader marked with a PTT, a study on the northward migration of Eastern Curlews moving from Australia to Arctic breeding grounds. Driscoll & Ueta (2002) marked birds >900 g with PTT's that weighed ~30 g (including the harness). That study was only partly successful because the harness-mounted PTT apparently hindered the bird's flight. In the coming years, studies of waders marked with smaller PTTs will undoubtedly elucidate a great deal about the ecology of large waders, especially their movements over large distances.

Another satellite application that may have future implications for waders as the size of units decrease are Global Positioning System (GPS) units such as those placed on Wandering Albatrosses *Diomedea exulans* (Weimerskirch *et al.* 2002). GPS transmitters are receiving units that scan for signals from a subset of 24 earth-orbiting satellites and then translate those signals into locations that are stored in the GPS unit (Merrill *et al.* 1998, Takekawa & Orthmeyer 2001). One of the limitations of this technique is that the data in the GPS unit generally has to be retrieved in many units. However, a recently developed 70 g solar transmitter included GPS locations and Argos downloading capabilities (Microwave Telemetry, Inc.). Unlike PTTs, GPS tags are very accurate (e.g. <5 m error).

There are other technologies that have applications for studying waders such as passive integrated transponder (PIT) tags. PIT tags can be quite small (18 mm long and 2 mm in diameter, Boarman *et al.* 1998) because their size is not increased by a power source. Instead, they are energized by an electromagnetic field coming from a transceiver antenna. PIT tags might be best adapted for the study of nesting waders, since they require the animal to come within a few centimetres of a transceiver (Boarman *et al.* 1998). A recent study of waders used PIT tags to examine incubation schedules of Kentish Plovers (syn. with Snowy Plover, Kosztolányi & Székely 2002). The 0.4 g transponders were glued to the tail feathers of incubating adult Kentish Plovers, and a reader and a computer were used to record, every 20s, whether a bird was incubating. Cresswell *et al.* (in press) used a similar system to study the incubation behaviour of Semipalmated Sandpipers, although the PIT tag was epoxied to the outer surface of a leg band.

Radio transmitters also may be equipped with sensors to provide additional information. For example, temperature is regularly recorded through variation in pulse rate, as is activity or posture. Mortality sensors typically double the pulse rate of the transmitter after a set period of inactivity. Alternatively temperature sensing can be used to detect loss of body heat when the animal dies. Pressure sensors may be used to examine elevation changes.

TYPES OF ATTACHMENTS

One of the most critical aspects in conducting radio telemetry studies is the attachment of the transmitter to the bird. There are basically four ways to affix a transmitter to a wader: 1) gluing the transmitter to the bird; 2) fastening the transmitter to a harness or band; 3) attaching the transmitter subcutaneously to the bird with sutures or prongs; or, 4) implanting the transmitter in the bird surgically. Each method has its advantages and disadvantages depending on the topic of interest and the species of wader under consideration.

Glue

The most common attachment method for waders has been to glue the transmitter onto the bird as described by Hill & Talent (1990) and Warnock & Warnock (1993). Advantages of gluing transmitters directly to birds is that it can be done relatively quickly, it can be done cheaply, the transmitter will eventually drop off, and there seems to be fewer behaviour effects compared to harness or implant techniques (Perry *et al.* 1981, Schulz *et al.* 2001, Bowman *et al.* 2002). Johnson *et al.* (1997, 2001) have shown that Pacific Golden-Plovers radio-marked in Hawaii and tracked to breeding grounds in Alaska have high return rates to Hawaii, indicating no long-term adverse effect of the radios. The disadvantage to gluing is that the transmitters generally stay on the bird for relatively short periods of time ranging from a few weeks to around four months, and retention time can vary by species and the moult schedule of the bird (Rohweder 1999; for non-waders see Johnson *et al.* 1991, Schulz *et al.* 2001).

Researchers have used several methods to glue the transmitter to the bird. Some have glued the transmitter to feathers between the wings on the upper back of the bird without removing or cutting any feathers (Knopf & Rupert 1995, 1996, Drake *et al.* 2001). Others have glued the radio directly to the skin just above the uropygial gland of the bird after removing or cutting feathers (Warnock & Warnock 1993, Warnock & Takekawa 1995, Warnock & Bishop 1996). Rohweder (1999) looked at three glue attachment combinations (including use of gauze and trimming feathers) on ten different wader species, and found that trimming feathers resulted in longer attachment time.

Different types of glue have been used, but these generally fall into two types: epoxy and cyanoacrylate (commonly called Superglue). Warnock *et al.* (2001) alternated affixing transmitters to Dunlin and Short- and Long-billed Dowitchers using bird epoxy (Titan Corporation, now discontinued) or cyanoacrylate (QuickTite™ super glue, Loctite Corp.©, Rocky Hill CT) and found no difference in the performance of these two glues, although the study did not evaluate maximum retention time. The performance of Superglue can be greatly enhanced by the use of Superglue activator that causes Superglue to set instantly on contact with a treated surface (B. Cresswell pers.comm.).

Harness or band

Harnesses have been used in many studies to attach transmitters to legs, wings, necks, or backs of birds (Kenward 1987). Most shorebird studies with harnesses have been conducted on medium sized or large waders such as American Woodcock (Dunford & Owen 1973, Horton & Causey 1979, 1984), oystercatchers (Exo *et al.* 1996), or curlews (Redmond & Jenni 1986, Driscoll & Ueta 2002, but see Sanzenbacher *et al.* 2000, Keedwell 2001).

Perhaps the biggest advantage of harnesses is the length of time the transmitter remains on the bird (e.g. Schulz *et al.* 2001, Doerr & Doerr 2002). Many waterfowl studies have documented changes in behaviour of birds marked with harnesses. Disadvantages of harnesses may be significant for waders, sometimes resulting in reduced survival. For example, waders get their lower mandible caught in the harness. Three Killdeer outfitted with necklace harnesses had their mandibles caught in the elastic harness that looped around their necks, and one died before it could be recaptured to remove the harness (N. Warnock & L. Oring unpubl. data). Several Bristle-thighed Curlews equipped with backpack transmitters on Laysan Island caught their lower mandibles in harness straps and would have died had researchers not removed transmitters (Marks *et al.* 2002). Marks *et al.* (2002) also found that 6 of 11 adult Bristle-thighed Curlews fitted with harness-mounted transmitters on breeding grounds in Alaska did not return in subsequent years and presumably died. In contrast, 19 of 20 curlews fitted with small transmitters (3 g) sewn or glued to scapular feathers or leg bands on the breeding grounds returned and bred in subsequent years (Marks *et al.* 2002). In Eurasian Oystercatchers, there is a suggestion that birds equipped with harnesses are less likely to return to breeding sites in subsequent years than unharnessed birds (Exo *et al.* 1996).

The migratory behaviour of Eastern Curlews with harness-mounted satellite transmitters was hindered, causing birds to discontinue migration to Asian breeding grounds from wintering areas in Australia (Driscoll & Ueta 2002). However, harnesses are often the primary attachment option for satellite transmitters with upright antennas to maximize signal reception by satellites orbiting 160 km away. Leg loop harnesses that hold the tag on the sacrum (Rappole & Tipton 1991, Sanzenbacher *et al.* 2000) may prevent some of the difficulties reported with other harness methods. Recently, Sanzenbacher & Haig (2002a, 2002b) had good results tracking Dunlin and Killdeer around an agricultural region of Oregon with leg loop harnesses and observed no apparent short-term (a few months) effects, although long-term survivorship of birds was not measured. In trying to find a radio transmitter attachment suitable for downy chicks, Keedwell (2001) used leg-loop harnesses on chicks of Banded Dotterel (syn. with Double-banded Plover). While she found no apparent difference in growth of chicks with harnesses vs. those without, she did find three chicks entangled in the harness and concluded the method was not suitable for young chicks.

For large, long-legged waders such as avocets and stilts, transmitters may be glued to leg bands (Plissner *et al.* 1999, 2000a; Hickey 2002). The advantage of this method is that the transmitter will stay on indefinitely, but this is also its disadvantage.

Grant (2002) reported gluing transmitters to the base of the central tail feathers of adult Eurasian Curlews; however, he did not report on retention times. Although tail-mounts are one of the most widely used method to radio tag birds (B. Cresswell pers. comm.), they are infrequently used on waders because glue-mounting is normally a better option.

Suture or prong

Sutures and prongs have been used to attach transmitters to several species of birds (Wheeler 1991, Newman *et al.* 1999), but they have not been used on waders. An advantage of these methods is that the transmitter stays on longer than attachment with glue (e.g. in Red-winged Blackbirds *Agelaius phoeniceus*, Martin & Bider 1978). Additionally, subcutaneous attachment may be less disruptive to the behaviour of the study species than harnesses. Ducks with transmitters attached with suture and glue suffered less predation that those with transmitters attached with harnesses (Wheeler 1991). The disadvantage of sutures or prongs is that it may require more training, and guidance of a veterinarian may be required. Suturing transmitters has been done successfully with precocial chicks of gallinaceous birds (e.g. Sage Grouse *Centrocerus urophasianus*, Burkepile *et al.* 2002), and waterfowl (Wheeler 1991), suggesting that this may be a suitable method for wader chick studies.

Surgical implant

To reduce behaviour problems seen in birds fitted with harnesses or to increase retention time over glue, transmitters have been implanted in birds with internal or external antennas (Korschgen *et al.* 1984, 1996, Schulz *et al.* 2001). With the exception of one test in a Bristle-thighed Curlew (R. Gill pers. comm.), transmitters have not yet been implanted in waders. The disadvantage of implants is that signal radiation is very poor unless the tag antenna is external and free-standing (and even then this can be a problem, B. Cresswell pers. comm.). A further disadvantage is that birds have to be anaesthetised and highly trained personnel or veterinarians have to conduct the marking. Additionally, efforts have to be made to make the area of surgery as aseptic as possible. If the surgery is done improperly and under non-sterile conditions, the area where the transmitter is implanted may become infected (Korschgen *et al.* 1984, 1996, Schulz *et al.* 2001). It is likely that this attachment technique will be considered more often in wader studies when the mass of PTTs decrease to allow their use in more wader species and the signal range of implanted tags increases.

TRACKING

Tracking is done on foot with handheld antennas (<2 km), in vehicles mounted with antenna systems (2–5 km), with antennas mounted on fixed towers (5–10 km), or from aircraft equipped with external antennas (10–20 km). Coordinated studies have been conducted to create a network of listening stations during shorebird migration (Iverson *et al.* 1996, Warnock & Bishop 1996, Warnock *et al.* 2002). Automated radio-tracking systems (ARTS) on towers with data loggers have been used to scan for transmitters continuously. They have been tested on waders in Europe and Australia (Piersma *et al.* 2001). ARTS are able to detect birds continuously up to 4 km away (Green *et al.* 2002). They have been used to track local movements and habitat use of waders (Exo *et al.* 1992, Exo & Scheiffarth 1993, Battley 2000, 2002), and to follow migration (Green *et al.* 2002). Results of a recent exploratory workshop (January 2003 at the Royal Netherlands Institute for Sea Research, Texel) within the Bird Migration programme of the European Science Foundation, on "The use and future of automated radio-tracking systems (ARTS) in bird migration studies", indicated that these systems have the capacity to gather tremendous amounts of data pertaining to wader ecology in relatively short amounts of time. Studies using ARTS have been done on Red Knots, Great Knots, Bar-tailed Godwits, and Eurasian Oystercatchers (ARTS workshop, Texel, The Netherlands, 2003; agenda available from lead author).

RESEARCH TOPICS

The value of radio telemetry to wader ecology has been significant, ranging from better understanding of nocturnal behaviour (Thibault & McNeil 1995, Rompré & McNeil 1996, Sitters 2000, Rohweder 2001) to understanding how individual birds migrate across long stretches of their migratory pathways (Evans 1996, Iverson *et al.* 1996, Bishop & Warnock 1998, Green *et al.* 2002). Telemetry studies will continue to strengthen our knowledge of waders in many research areas, including space use, distribution, migration, survival, and population size.

Space use

Radio telemetry is ideally suited for understanding how and when organisms move about their landscape, and what habitats (as defined by Hall *et al.* 1997) are used within these landscapes (Brown & Orians 1970, White & Garrott 1990, Samuel & Fuller 1996, Villard *et al.* 1998, Kernohan *et al.* 2001). Local movements and habitat use of many wader species have been studied during breeding and non-breeding seasons (Table 1). A subset of these habitat studies has compared diurnal and nocturnal movements (Owen & Morgan 1975, Wood 1986, McNeil & Rompré 1995, Whittingham 1999a, Rohweder & Lewis 2001, Sitters *et al.* 2001), an area little studied prior to the advent of radio telemetry. Another area that radio telemetry has advanced is the study of movements and dispersal of wader chicks (Horton & Causey 1984, Redmond & Jenni 1986, Yalden 1991, Whittingham *et al.* 1999b, Grant 2002).

Several statistical methods have been developed to rigorously describe and analyse home range data from radio-marked animals (see White & Garrott 1990, Samuel & Fuller 1996, Millspaugh & Marzluff 2001). It is notable that relatively few telemetry wader studies have rigorously calculated home ranges, since these areas are valuable for conservation management as they encompass the essential needs for an individual's survival and reproduction (Burt 1943). Home ranges for certain upland game waders have been calculated (e.g. Eurasian Woodcock, American Woodcock, Great Snipe) and a few other species like Killdeer, Black-necked Stilt, Western Sandpiper, and Long-billed Dowitcher (Table 1). Most of these studies have been based in North America. This is clearly an area where much more work can be done.

Likewise, telemetry studies are well suited to examining habitat selection questions of habitat use vs. availability (Neu *et al.* 1974, Aebischer *et al.* 1993, Jones 2001), yet few rigorous studies of these types have been done on radio-marked waders, all in North America (see Knopf & Rupert 1995, Warnock & Takekawa 1995, Takekawa *et al.* 2002).

Migration

Given waders' propensity to stop at discrete bodies of water along their migratory flyways that can be searched fairly easily from the ground or air for radio-marked birds, they can be ideal organisms to track over distances of thousands of kilometres, using a host of collaborating researchers. Radio telemetry provides techniques to study migration routes, chronology, and stopover ecology of migratory birds. Studies of wader migration using radio telemetry began in the early 1990s (Skagen & Knopf 1994, Iverson *et al.* 1996) and have continued to be a source of new information on waders over larger scales (Driscoll & Ueta 2002, Warnock *et al.* 2002). These shorebird studies have tended to focus on two aspects of migration: 1) stopover ecology (Skagen & Knopf 1994, Warnock & Bishop 1996, Farmer & Parent 1997, Nebel *et al.* 2000), and 2) connectivity of areas within species's migratory flyway (Butler *et al.*1996, Evans 1996, Johnson *et al.* 1997, 2001, Haig *et al.* 2002).

However, there are logistic difficulties to consider in these types of studies. Tracking birds across international boundaries can present problems, especially when one is trying to track rapidly moving species. Keeping track of more than 100 different radio frequencies can be difficult since these radios tend to be small with short ranges (<5 km). A problem that has been particularly acute in North America in large-scale studies is overlapping radio frequencies with other wildlife studies. For instance, during migration studies of waders, these authors have discovered overlapped frequencies with radio-marked Marbled Murrelets *Brachyramphus marmoratus*, Northern Pintails *Anas acuta*, White-fronted Geese *Anser albifrons*, Golden Eagles *Aquila chrysaetos*, Surf Scoters *Melanitta perspicillata*, Harbor Seals *Phoca vitulina*, Moose *Alces alces*, and Caribou *Rangifer rangifer*. This problem is exacerbated by minimal national or international coordination of radio frequency use, and it only promises to get worse.

Behaviour

Radio transmitters are useful for studying the breeding behaviour of species that are secretive. For example, early studies of upland game birds were often used to locate nests (Schemnitz & Owen 1969, Marshall *et al.* 1971, Ramakka 1971, 1972, Tuck 1972). Core areas (50% use areas) within home ranges have often been used to identify primary use sites during the breeding season. In conjunction with behaviour observations or motion sensors, radio telemetry also may be used to estimate the proportion of time spent foraging in different habitats. Pressure sensors provide a means to examine elevations used during local movements and migration flights.

Population dynamics

Radio telemetry can be an ideal tool for estimating survival in marked animals (White & Garrott 1990, Samuel & Fuller 1996). One advantage of using radio-marked individuals for survival studies vs. using banded individuals is that capture probabilities do not have to be modelled (e.g. Lebreton *et al.* 1992) since within given areas radio-marked individuals (both dead and alive) can be relocated with near certainty (Tsai *et al.* 1999), and suitable analysis methods have been developed (White & Garrott 1990, Samuel & Fuller 1996, Tsai *et al.* 1999). It is interesting, that with the exception of studies of one upland game species, the American Woodcock (Derleth & Sepik 1990, Krementz *et al.* 1994, Longcore *et al.*1996, Krementz & Berdeen 1997), very little has been published on survival rates of radio-marked waders (but see Knopf & Rupert 1995, Drake *et al.* 2001, Table 1). Studies based on radio-marked birds have the potential to greatly expand our knowledge of survival of waders during different parts of the year and from different areas of the world, information lacking for most wader species (Evans 1991).

Radio-marked individuals, especially those with mortality sensors (motion, temperature), may be used to determine cause-of-death. Recoveries are possible for individuals that do not die in salt water, including finding remains left by predators. This may be especially useful in harvested populations (legal or illegal) if behaviour of radio-marked birds does not differ and they are taken proportional to the harvest. Although it is possible to examine fresh carcasses and determine cause of death such as some disease, other causes of death such as predation may require detailed examination of the area to separate predation from scavenging.

Radio telemetry may be used to estimate population size for species that are difficult to observe, such as snipes and woodcocks. Program NOREMARK (White 1996) allows calculation of total population and a daily population estimate from radio relocations over survey periods. Assumptions for this estimator include: 1) the number of animals is constant within each survey period, 2) relocation probability is the same for all animals, 3) animals are sampled once in a survey, 4) the sample is from an open population, and 5) the sample fits a joint hypergeometric maximum-likelihood distribution adjusted for immigration and emigration.

Future directions

There is still much that telemetry studies of waders can contribute to their conservation, management and a better understanding of their ecology. Most wader species have never been the focus of a telemetry study despite the fact that the technique has the ability to gather data that are otherwise difficult to collect. There has never been a telemetry study of waders in Africa and little work has been done in South America or Asia. Little research has been done using transmitters with sensors built into them (e.g. Exo *et al.* 1992). Telemetry units that collect data such as body temperatures or heart rates could be incorporated into larger telemetry units to better understand the physiology of waders under different environmental conditions during different phases of their year.

At the recent ARTS workshop (see description in Tracking section) exciting discussions were held on advances in radio telemetry technology. Alejandro Purgue (Cornell University) spoke of developing small (a few grams and smaller) digital transmitters to be used with ART systems that could be programmed to turn on and off again on any number of schedules (such as turn off on weekends and from 1800–0400). Martin Wikelski (Princeton University) and George Swenson (University of Illinois) spoke on the feasibility of attaching large antennae to the International Space Station and using them with automatic tracking equipment to follow birds equipped with small VHF and digital transmitters from space. The workshop demonstrated that, technologically, we are immersed in a rapidly evolving and exciting time. Through the use of telemetry, the near future will likely expose details of the ecology of waders that previously have been unattainable.

ACKNOWLEDGEMENTS

We dedicate this paper to the memory of Peter R. Evans, whose early conversations with the senior author on the migration of waders continue to be an inspiration. Thanks to Jim Ramakka, R. Bucky Owen and Bill Krohn for help with tracking down early references to shorebird telemetry studies. Input from N. Athearn, B. Cresswell, M. Exo, R. Gill, C. Gratto-Trevor, K. Phillips, B. Sandercock, and ARTS workshop participants is greatly appreciated. Editorial comments by B. Cresswell improved an earlier version of this manuscript. This is a contribution of PRBO Conservation Science (#1000) and the U.S. Geological Survey.

REFERENCES

Aebischer, N.J., Robertson, P.A. & Kenward, R.E. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74: 1313–1325.

Ailes, I.W. & Toepfer, J.E. 1977. Home range and daily movements of radio-tagged Upland Sandpipers in central Wisconsin. *Inland Bird Banding News* 49: 203–212.

Baker, A.J., González, P.M., Piersma, T., Minton, C.D.T., Wilson, J.R., Sitters, H., Graham, D., Jessop, R., Collins, P., de Goeij, P., Peck, M.K., Lini, R., Bala, L., Pagnoni, G., Vila, A., Bremer, E., Bastida, R., Ieno, E., Blanco, D., de Lima, S., Do Nascimento, I., Scherer, S.S., Schnieder, M.P., Silva, A. & Rodriguez, A.A.F. 1999. Northbound migration of Red Knots *Calidris canutus rufa* in Argentina and Brazil: report on results obtained by an international expedition in March–April 1997. *Wader Study Group Bull.* 88: 64–75.

Battley, P. 2000. Radio-tracking in the tropics. *The Tattler* 25: 3–5.

Battley, P. 2002. Behavioural ecophysiology of migratory Great Knots. Ph.D. dissertation, Griffith University, Australia.

Berdeen, J.B. & Krementz, D.G. 1998. The use of fields at night by wintering American woodcock. *J. Wildlife Management* 62: 939–947.

Bishop, M.A. & Warnock, N. 1998. Migration of Western Sandpipers: links between their Alaskan stopover areas and breeding grounds. *Wilson Bull.* 110: 457–462.

Boarman, W.I., Beigel, M.L., Goodlett, G.C. & Sazaki, M. 1998. A passive integrated transponder system for tracking animal movements. *Wildlife Soc. Bull.* 26: 886–891.

Bowman, J., Wallace, M.C., Ballard, W.B., Brunjes IV, J.H., Miller, M.S. & Hellman, J.M. 2002. Evaluation of two techniques for attaching radio transmitters to turkey poults. *J. Field Ornith.* 73: 276–280.

Brown, J.L. & Orians, G.H. 1970. Spacing patterns in mobile animals. Pages 239–262 *in* R.F. Johnson, editor. *Annual review of ecology and systematics.* Annual Review, Inc., Palo Alto.

Burkepile, N.A., J.W. Connelly, D.W. Stanley & K.P. Reese. 2002. Attachment of radiotransmitters to one-day-old sage grouse chicks. *Wildlife Soc. Bull.* 30: 93–96.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *J. Mammalogy* 24: 346–352.

Burton, N.H.K. 2000. Winter site-fidelity and survival of Redshank *Tringa totanus* at Cardiff, south Wales. *Bird Study* 47: 102–112.

Butler, R.W., Delgado, F.S., de la Cueva, H., Pulido, V. & Sandercock, B.K. 1996. Migration routes of the Western Sandpiper. *Wilson Bull.* 108: 662–672.

Byrkjedal, I. 1985. Time-activity budget for breeding Greater Golden-Plovers in Norwegian mountains. *Wilson Bull.* 97: 486–501.

Caccamise, D.F. & Hedin, R.S. 1985. An aerodynamic basis for selecting transmitter loads in birds. *Wilson Bull.* 97: 306–318.

Colwell, M.A. & Oring, L.W. 1988. Variable female mating tactics in a sex-role-reversed shorebirds, Wilson's Phalarope (*Phalaropus tricolor*). *Nat. Geog. Res.* 4: 408–415.

Coon, R.A., Caldwell, P.D. & Storm, G.L. 1976a. Onset of fall migration of radio-marked woodcock with notes on a portion of the migratory flight of one bird. *Proc. 5th American Woodcock Workshop*.

Coon, R.A., Caldwell, P.D. & Storm, G.L. 1976b. Some characteristics of fall migration of female woodcock. *J. Wildlife Management* 40: 91–95.

Cresswell, M.A. & Summers, R.W. 1988. A study of breeding Purple Sandpipers *Calidris maritima* on the Hardangervidda using radio-telemetry. *Norvegica Series C Cinclus* 11: 1–6.

Cresswell, W., Holt S., Reid, J.M., Whitfield, D.P. & Mellanby, R.J. In press. Do energetic demands constrain incubation scheduling in a biparental species? *Beh. Ecol.* 14.

Del Hoyo, J.A., Elliott, A. & Sargatal, J., Eds. 1996. *Handbook of the birds of the world. Vol. 3. Hoatzin to auks.* Lynx Edicions, Barcelona.

Derleth, E.L. &. Sepik, G.F. 1990. Summer–fall survival of American Woodcock in Maine. *J. Wildlife Management* 54: 97–106.

Doerr, V.A.J. & Doerr, E.D. 2002. A dissolving leg harness for radio transmitter attachment in treecreepers. *Corella* 26: 19–21.

Drake, K.R., Thompson, J.E., Drake, K.L. & Zonick, C. 2001. Movements, habitat use, and survival of nonbreeding Piping Plovers. *Condor* 103: 259–267.

Driscoll, P. & Minton, C. 1999. Eastern Curlew coming "home". *The Tattler* 20: 4.

Driscoll, P.V. & Ueta, M. 2002. The migration and behaviour of Eastern Curlews *Numenius madagascariensis. Ibis* 144 (on-line): E119–E130.

Dugan, P.J. 1981. The importance of nocturnal foraging in shorebirds: a consequence of increased invertebrate prey activity. Pages 251–260 *in* Jones, N.V. & Wolff, W.J. editors. *Feeding and survival strategies of estuarine organisms.* Plenum Press, New York.

Dunford, R.D. & Owen, R.B. 1973. Summer behavior of immature radio-equipped woodcock in central Maine. *J. Wildlife Management* 37: 462–469.

Evans, P.R. 1991. Seasonal and annual patterns of mortality in migratory shorebirds: some conservation implications. Pages 346–359 *in* J.-D. & L.C.M. Perrins, and G.J.M. Hirons, editor. *Bird population studies.* Oxford University Press, Oxford.

Evans, P.R. 1996. Radio-controlled Sanderlings. *Wader Study Group Bull.* 80: 6.

Exo, K.-M. 1992. Methoden zur Aufnahme von Raum-Zeit-Budgets bei Vögeln, dargestellt am Beispiel des Austernfischers (*Haematopus ostralegus*). *Vogelwarte* 36: 311–325.

Exo, K.-M. 1993. Methods to monitor time and energy budgets of birds, especially waders (Charadriiformes). *Proc. XII International Symposium on Biotelemetry* August 31–September 5, Ancona, Italy: 224–231.

Exo, K.-M., Eggers, U., Laschefski-Sievers, R. & Scheiffarth, G. 1992. Monitoring activity patterns using a micro-computer-controlled radiotelemetry system, tested for waders (Charadrii) as an example. Priede, I.G., and S.M. Swift, eds. *Wildlife telemetry, remote monitoring and tracking of animals* Ellis Horwood, Chinchester: 79–87.

Exo, K.-M. & Scheiffarth, G. 1993. The application of motion sensitive transmitters to record activity and foraging patterns of oystercatchers. *Limosa* 66: 80.

Exo, K.-M., Scheiffarth, G., & Haesihus, U. 1996. The application of motion sensitive transmitters to record activity and foraging patterns of oystercatchers *Haematopus ostralegus. Ardea* 84A: 29–38.

Farmer, A.H. & Parent, A.H. 1997. Effects of landscape on shorebird movements at spring migration stopovers. *Condor* 99: 698–707.

Farmer, A.H. & Wiens, J.A. 1999. Models and reality: time–energy trade-offs in Pectoral Sandpipers (*Calidris melantos*) migration. *Ecology* 80: 2566–2580.

Gabbard, C., Sprandel, G. & Cobb, D. 2001. Home range analyses of shorebirds wintering along the Gulf of Mexico, Florida, USA. *Wader Study Group Bull.* 96: 79–85.

Gill, R.E., Lanctot, R.B., Mason, J.D. & Handel, M.C. 1991. Observations on habitat use, breeding chronology and parental care in Bristle-thighed Curlews on the Seward Peninsula, Alaska. *Wader Study Group Bull.* 61: 28–36.

Gill, R.E., Jr., Tomkovich, P.S. & Dementyev, M.N. 1999. Breeding ecology of Surfbirds (*Aphriza virgata*) at Turquoise Lake, Alaska, 1997–1999 with observations of nesting Wandering Tattlers (*Heteroscelus incanus*) and annotated notes of birds and mammals. Unpubl. Report, U.S. Geological Survey, Alaska Biol. Sci. Center, Anchorage, AK.

Grant, M.C. 2002. Effects of radiotagging on the weight gain and survival of Curlew *Numenius arquata* chicks. *Bird Study* 49: 172–176.

Green, M., Piersma, T., Jukema, J., De Goeij, P., Spaans, B. & van Gils, J. 2002. Radio-telemetry observations of the first 650 km of the migration of Bar-tailed Godwits *Limosa lapponica* from the Wadden Sea to the Russian Arctic. *Ardea* 90: 71–80.

Gregg, L. 1984. Population ecology of woodcock in Wisconsin. *Wisconsin Department of Natural Technical Bulletin Series*, No. 144: 51 pp.

Haig, S.M., Oring, L.W., Sanzenbacher, P.M. & Taft, O.W. 2002. Space use, migratory connectivity, and population segregation among Willets breeding in the western Great Basin. *Condor* 104: 620–630.

Hall, L.S., Krausman, P.R. & Morrison, M.L. 1997. The habitat concept and a plea for standard terminology. *Wildlife Soc. Bull.* 25: 173–182.

Hickey, C.M. 2002. Black-necked Stilt (*Himantopus mexicanus*) space use and site fidelity in the San Francisco Bay Estuary: toward predicting shorebird response to salt pond conversions. M.S. thesis, University of California, Davis.

Hill, L.A. & Talent, L.G. 1990. Effects of capture, handling, banding, and radio-marking on breeding Least Terns and Snowy Plovers. *J. Field Ornith.* 61: 310–319.

Hirons, G.J.M. & Owen, Jr., R.B. 1982. Radio tagging as an aid to the study of Woodcocks. *Symp. Zool. Soc. Lond.* 49: 139–152.

Höglund, J. & Robertson, J.G.M. 1990. Spacing of leks in relation to female home ranges, habitat requirements and male attentiveness in the great snipe (*Gallinago media*). *Behav. Ecol. Sociobiol.* 26: 173–180.

Hoodless, A., Draycott, R.A.H. & Tucker, K. 2000. Winter habitat-use and diet of the Common Snipe (*Gallinago gallinago*) in south-west England.

Wetlands International Global Series No. 4, International Wader Studies 11: 57–66.

Horton, G.I. & Causey, M.K. 1979. Woodcock movements and habitat utilization in central Alabama. *J. Wildlife Management* 43: 414–420.

Horton, G.I. & Causey, M.K. 1984. Brood abandonment by radio-tagged American Woodcock hens. *J. Wildlife Management* 48: 606–607.

Hudgins, J.E., Storm, G.L. & Wakeley, J.S. 1985. Local movements and diurnal-habitat selection by male American woodcock in Pennsylvania. *J. Wildlife Management* 49: 614–619.

Iverson, G.C., Warnock, S.E., Butler, R.W., Bishop, M.A. & Warnock, N. 1996. Spring migration of Western Sandpipers along the Pacific Coast of North America. *Condor* 98: 10–21.

Johnson, G.D., Pebworth, J.L. & Krueger, H.O. 1991. Retention of transmitters attached to passerines using a glue-on technique. *J. Field Ornith.* 62: 486–491.

Johnson, O.W., Warnock, N., Bishop, M.A., Bennet, A.J., Johnson, P.M. & Kienholz, R.J. 1997. Migration by radio-tagged Pacific Golden-Plovers from Hawaii to Alaska and their subsequent survival. *Auk* 114: 521–524.

Johnson, O.W., Bennett, A.J., Alsworth III, L., Bennett, L.A., Johnson, P.M., Morgart, J.R. & Kienholz, R.J. 2001. Radio-tagged Pacific Golden-Plovers: the Hawaii–Alaska link, spring destinations, and breeding season survival. *J. Field Ornith.* 72: 537–546.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. *Auk* 118: 557–562.

Kålås, J.A., Løfaldi, L. & Fiske, P. 1989. Effects of radio packages on Great Snipe during breeding. *J. Wildlife Management* 53: 1155–1158.

Keedwell, R. 2001. Evaluation of radio transmitters for measuring chick mortality in the Banded Dotterel. *Waterbirds* 24: 217–223.

Kenward, R. 1987. *Wildlife radio tagging*. Academic Press, London.

Kernohan, B.J., Gitzen, R.A. & Millspaugh, J.J. 2001. Analysis of animal space use and movements. Pages 125–166 *in* J.J. Millspaugh, editor. *Radio tracking and animal populations*. Academic Press, San Diego, CA.

Ketzenberg, C. & Exo, K.-M. 1996. Habitat choice of migrating Golden Plovers (*Pluvialis apricaria*). *Verh. Dtsch. Zool. Ges.* 89: 309.

Ketzenberg, C. & K.-M. Exo. 1997. Windenergieanlagen und Raumansprüche von Küstenvögeln. *Natur und Landschaft* 72: 352–357.

Knopf, F.L. & Rupert, J.R. 1995. Habits and habitats of Mountain Plovers in California. *Condor* 97: 743–751.

Knopf, F.L. & Rupert, R.J. 1996. Reproduction and movements of Mountain Plovers breeding in Colorado. *Wilson Bull.* 108: 28–35.

Korschgen, C.E., Maxson, S.J. & Kuechle, V.B. 1984. Evaluation of implanted radio transmitters in ducks. *J. Wildlife Management* 48: 982–987.

Korschgen, C.E., Kenow, K.P., Gendron-Fitzpatrick, A., Green, W.L. & Dein, F.J. 1996. Implanting intra-abdominal radiotransmitters with external whip antennas in ducks. *J. Wildlife Management* 60: 132–137.

Kosztolányi , A. & Székely, T. 2002. Using a transponder system to monitor incubation routines of snowy plovers. *J. Field Ornithology* 73: 199–205.

Krementz, D.G. & Berdeen, J.B. 1997. Survival rates of American Woodcock wintering in the Georgia Piedmont. *J. Wildlife Management* 61: 1328–1332.

Krementz, D.G. & Pendleton, G.W. 1994. Diurnal habitat use of American Woodcock wintering along the Atlantic Coast. *Canadian J. Zool.* 72: 1945–1950.

Krementz, D.G., Seginak, J.T., Smith, D.R. & Pendleton, G.W. 1994. Survival rates of American Woodcock wintering along the Atlantic Coast. *J. Wildlife Management* 58: 147–155.

Krementz, D.G., Seginak, J.T. & Pendleton, G.W. 1995. Habitat use at night by wintering American Woodcock in coastal Georgia and Virginia. *Wilson Bull.* 107: 686–697.

Lanctot, R.B. 1994. Blood sampling in juvenile Buff-breasted Sandpipers: movement, mass change and survival. *J. Field Ornith.* 65: 534–542.

Lanctot, R.B., Scribner, K., Kempenaers, B. & Weatherhead, P.J. 1997. Lekking without a paradox in the Buff-breasted Sandpiper. *American Naturalist* 149: 1051–1070.

Lanctot, R.B., Weatherhead, P.J., Kempenaers, B. & Scribner, K.T. 1998. Male traits, mating tactics and reproductive success in the Buff-breasted Sandpiper, *Tryngites subruficollis*. *Animal Behaviour* 56: 419–432.

Lang, L. 1994. Woodcock migration study. Pennsylvania Game News Final Report: 6 pp.

Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62: 67–118.

Longcore, J.R., McAuley, D.G., Sepik, G.F. & Pendleton, G.W. 1996. Survival of breeding male American woodcock in Maine. *Canadian J. Zool.* 74: 2046–2054.

Marks, J.S., Tibbitts, T.L., Gill, Jr., R.E. & McCaffery, B.J. 2002. Bristle-thighed Curlew (*Numenius tahitiensis*). In *The birds of North America*, No. 706 (A. Poole and F. Gill, eds.). Philadelphia: The Academy of Natural Sciences; Washington D.C.: The American Ornithologists' Union.

Marshall, W.H., Godfrey, G.A. & Wenstrom, W.P. 1971. Minnesota telemetry studies. *In* Fourth American Woodcock Workshop proceedings. Higgins Lake, Michigan. Oct. 13–15, 1971.

Martin, M.L. & Bider, J.R. 1978. Transmitter attachment for blackbirds. *J. Wildlife Management* 42: 613–685.

McAuley, D.G., Longcore, J.R. & Sepik, G.F. 1993a. Techniques for research into woodcocks: experience and recommendations. *In* J.R. Longcore and G.F. Sepik, eds. *Eighth woodcock symposium* U.S. Fish and Wildlife Service Biological Report 16: 5–11.

McAuley, D.G., Longcore, J.R. & Sepik, G.F. 1993b. Behavior of radio-marked breeding American Woodcocks. *In* J.R. Longcore and G.F. Sepik, eds. *Eighth woodcock symposium* U.S. Fish and Wildlife Service Biological Report 16: 116–125.

McNeil, R. & Rompré, G. 1995. Day and night feeding territoriality in Willets *Catoptrophorus semipalmatus* and Whimbrel *Numenius phaeopus* during the non-breeding season in the tropics. *Ibis* 137: 169–176.

Merrill, S.B., Adams, L.G., Nelson, M.E. & Mech, L.D. 1998. Testing releasable GPS radiocollars on wolves and white-tailed deer. *Wildlife Soc. Bull.* 26: 830–835.

Miller, B.J. & Knopf, F.L. 1993. Growth and survival of Mountain Plovers. *J. Field Ornith.* 64: 500–506.

Millspaugh, J.J. & Marzluff, J.M. 2001. *Radio tracking and animal populations*. Academic Press, San Diego, CA.

Minton, C. & Driscoll, P. 1999. Eastern Curlews on track again. *The Tattler* 19: 2.

Nebel, S., Piersma, T., Van Gils, J., Dekinga, A. & Spaans, B. 2000. Length of stopover, fuel storage and a sex-bias in the occurence of Red Knots *Calidris c. canutus* and *C. c. islandica* in the Wadden Sea during southward migration. *Ardea* 88: 165–176.

Neu, C.W., Byers, C.R. & Peek, J.M. 1974. A technique for analysis of utilization–availability data. *J. Wildlife Management* 38: 541–545.

Newman, S.H., Takekawa, J.Y., Whitworth, D.L. & Burkett, E.E. 1999. Subcutaneous anchor attachment increases retention of radio transmitters on Xantus' and Marbled murrelets. *J. Field Ornith.* 70: 520–534.

Niles, L.W., Peck, M. & Lathrop, R. 2001. Breeding habitat of the Red Knot in Nunavut, Canada. *Wader Study Group Bull.* 95: 14 (abstract).

Owen, R.B., Jr. & Morgan, J.W. 1975. Summer behavior of adult radio-equipped woodcock in central Maine. *J. Wildlife Management* 39: 179–182.

Pace, R.M., III. 2000. Winter survival rates of American woodcock in south central Louisiana. *J. Wildlife Management* 64: 933–939.

Pedersen, M.B. 1995. Opportunistic behaviour as key-determinant in the winter strategy of the Jack Snipe *Lymnocryptes minimus* in southern Scandinavia. *Wader Study Group Bull.* 78: 23–26.

Perry, M.C., Haas, G.H. & Carpenter, J.W. 1981. Radio transmitters for mourning doves: comparisons of attachment techniques. *J. Wildlife Management* 45: 524–527.

Piersma, T., Spaans, B. & Dekinga, A. 2001. ARTS and science: the use of automated radio tracking stations to study the movements of shorebirds. *Wader Study Group Bull.* 95: 17 (abstract).

Plissner, J.H., Haig, S.M. & Oring, L.W. 1999. Within- and between-year dispersal of American Avocets among multiple western Great Basin wetlands. *Wilson Bull.* 111: 314–320.

Plissner, J.H., Haig, S.M. & Oring, L.W. 2000a. Post-breeding movements of American Avocets and implications for wetland connectivity in the western Great Basin. *Auk* 117: 290–298.

Plissner, J.H., Oring, L.W. & Haig, S.M. 2000b. Space use of Killdeer at a Great Basin breeding area. *J. Wildlife Management* 64: 421–429.

Powers, L.C. 1998. Space use of breeding Killdeer *Charadrius vociferus*. MSc thesis, University of Nevada, Reno.

Ramakka, J.M. 1971. Breeding season behavior of radio-equipped male woodcock. M.S. thesis, University of Maine, Orono.

Ramakka, J.M. 1972. Effects of radio-tagging on breeding behavior of male woodcock. *J. Wildlife Management* 36: 1309–1312.

Rappole, J.H. & Tipton, A.R. 1991. New harness design for attachment of radio transmitters to small passerines. *J. Field Ornith.* 62: 335–337.

Redmond, R.L. 1984. The behavioral ecology of Long-billed Curlews breeding in western Idaho. Unpublished Ph.D. dissertation, University of Montana, Missoula.

Redmond, R.L. & Jenni, D.A. 1986. Population ecology of the Long-billed Curlew (*Numenius americanus*) in western Idaho. *Auk* 103: 755–767.

Robson, G. 1998. The breeding ecology of Curlew *Numenius arquata* on north Pennine moorland. Ph.D. dissertation, University of Sunderland.

Rohweder, D.A. 1999. Evaluation of three methods used to attach radio-transmitters to waders. *Corella* 23: 7–10.

Rohweder, D.A. 2001. Nocturnal roost use by migratory waders in the Richmond River Estuary, northern New South Wales, Australia. *Stilt* 40: 23–28.

Rohweder, D.A. & Lewis, B.D. 2001. Day–night habitat use by Double-banded Plovers *Charadrius bicinctus* in the Richmond River Estuary, northern New South Wales. *Corella* 26: 33–37.

Rompré, G. & McNeil, R. 1996. Variability in day and night feeding habitat use in the Willet *Catoptrophorus semipalmatus* during the non-breeding season in northeastern Venezuela. *Wader Study Group Bull.* 81: 82–87.

Samuel, M.D. & Fuller, M.R. 1996. Wildlife radiotelemetry. Pages 370–418 *in* T.A. Bookhout, editor. *Research and management techniques for wildlife and habitats. Fifth edition, revised.* The Wildlife Society, Bethesda, MD.

Sanzenbacher, P.M., Haig, S.M. & Oring, L.W. 2000. Application of a modified harness design for attachment of radio transmitters to shorebirds. *Wader Study Group Bull.* 91: 16–20.

Sanzenbacher, P.M. & Haig, S.M. 2002a. Residency and movement patterns of wintering Dunlin in the Willamette Valley of Oregon. *Condor* 104: 271–280.

Sanzenbacher, P.M. & Haig, S.M. 2002b. Regional fidelity and movement patterns of wintering Killdeer in an agricultural landscape. *Waterbirds* 25: 16–25.

Schemnitz, S.D. & Owen, Jr., R.B. 1969. Pilot radio-telemetry studies of woodcock in Maine. Paper presented at the 3rd American Woodcock Workshop, July 2, 1969, Orono, Maine.

Schulz, J.H., Bermudez, A.J., Tomlinson, J.T., Firman, J.D. & He, Z. 2001. Comparison of radiotransmitter attachment techniques using captive mourning doves. *Wildlife Soc. Bull.* 29: 771–782.

Shepherd, P. 2001. Space use, habitat preferences, and time–activity budgets of non-breeding Dunlin *Calidris alpina pacifica* in the Fraser River Delta, B.C. PhD dissertation, Simon Fraser University, Burnaby.

Sitters, H.P. 2000. The role of night-feeding in shorebirds in an estuarine environment with specific reference to mussel-feeding Oystercatchers. D.Phil dissertation, University of Oxford.

Sitters, H.P., Gonzalez, P.M., Piersma, T., Baker, A.J. & Price, D.J. 2001. Day and night feeding habitat of Red Knots in Patagonia: profitability versus safety? *J. Field Ornith.* 72: 86–95.

Skagen, S.K. & Knopf, F.L. 1994. Residency patterns of migrating sandpipers at a midcontinental stopover. *Condor* 96: 949–958.

Smart, J. & Gill, J.A. 2002. Turnstones and wheat: vegetarianism or problems with intertidal prey? *Wader Study Group Bull.* 99: 11–12 (abstract).

Smart, J. & Gill, J.A. in press. Non-intertidal habitat use by shorebirds: a reflection of inadequate intertidal resources? *Biological Conservation.*

Smith, K.W. 1987. What do Green Sandpipers do at night? *Wader Study Group Bull.* 51: 22–23 (abstract).

Smith, K.W., Reed, J.M. & Trevis, B.E. 1999. Nocturnal and diurnal activity patterns and roosting sites of Green Sandpipers *Tringa ochropus* wintering in southern England. *Ringing & Migration* 19: 315–322.

Storm, G.L. & Wakeley, J.S. 1981. Habitat selection by radio-tagged male woodcock in central Pennsylvania. Final report for U.S. Fish and Wildlife Services contract with the Pennsylvania Game Commission.

Summers, R. 1994. Diurnal and nocturnal activities of a Purple Sandpiper *Calidris maritima. Wader Study Group Bull.* 72: 33–34.

Takekawa, J.Y. & Orthmeyer, D.L. 2001. Application of radio telemetry in studies of cranes. Pages 85–98 *in* Z.H.R.L. Johnson, and R.C. Stendell, editor. *Cranes in East Asia: proceedings of the symposium.* U.S. Geological Survey, Midcontinent Ecological Service Center, Fort Collins, CO, Harbin, People's Republic of China. June 9–18, 1998.

Takekawa, J.Y., Warnock, N., Martinelli, G.M., Miles, A.K. & Tsao, D.C. 2002. Waterbird use of bayland wetlands in the San Francisco Bay Estuary: movements of Long-billed Dowitchers during winter. *Waterbirds* 25 (Special Publication 2): 93–105.

Thibault, M. & McNeil, R. 1995. Day- and night-time parental investment by incubating Wilson's Plovers in a tropical environment. *Canadian J. Zool.* 73: 879–886.

Todd, M.K. 2000. Feeding ecology of Latham's Snipe *Gallinago hardwickii* in the Lower Hunter Valley. *Emu* 100: 133–138.

Tsai, K., Pollock, K.H. & Brownie, C. 1999. Effects of violation of assumptions for survival analysis methods in radiotelemetry studies. *J. Wildlife Management* 63: 1369–1375.

Tuck, L.M. 1972. The snipes: a study of the genus *Capella*. Canadian Wildlife Service Monograph Series – No. 5, Halifax.

Tulp, I., Schekkerman, H., Piersma, T., Jukema, J., de Goeij, P. & van de Kam, J. 1998. Breeding waders at Cape Sterlegova, northern Taimyr, in 1994. WIWO-report, Zeist.

Van Gils, J. & Piersma, T. 1999. Day- and night-time movements of radiomarked Red Knots staging in the western Wadden Sea in July–August 1995. *Wader Study Group Bull.* 89: 36–44.

Villard, M.-A., Schmidt, E.V. & Maurer, B.A. 1998. Contribution of spatial modeling to avian conservation. Pages 49–64 *in* J. Marzluff & R. Sallabanks, editor. *Avian conservation: research and management.* Island Press, Washington, D.C.

Warnock, N. 1996. Local and regional differences in habitat utilization by Dunlins *Calidris alpina* as revealed by radio-telemetry: conservation implications. *International Wader Studies* 8: 35–38.

Warnock, N. & Warnock, S. 1993. Attachment of radio-transmitters to sandpipers: review and methods. *Wader Study Group Bull.* 70: 28–30.

Warnock, N., Page, G.P. & Stenzel, L.E. 1995. Non-migratory movements of Dunlin on their California wintering grounds. *Wilson Bull.* 107: 131–139.

Warnock, N. & Bishop, M.A. 1996. Spring stopover ecology of migrant Western Sandpipers. *Condor* 100: 456–467.

Warnock, N. & Oring, L.W. 1996. Nocturnal nest attendance of Killdeers: more than meets the eye. *Auk* 113: 502–504.

Warnock, N., Bishop, M.A. & Takekawa, J.Y. 2001. Spring migration of Dunlin and dowitchers along the Pacific Flyway. Unpubl. Prog. Report, Point Reyes Bird Observatory, Stinson Beach, CA, and U.S. Geological Survey, Vallejo, CA.

Warnock, N., Bishop, M.A. & Takekawa, J.Y. 2002. Spring shorebird migration from Mexico to Alaska. Final report 2002. Unpubl. Prog. Report, Point Reyes Bird Observatory, Stinson Beach, CA, and U.S. Geological Survey, Vallejo, CA.

Warnock, S.E. & Takekawa, J.Y. 1995. Habitat preferences of wintering shorebirds in a temporally changing environment: Western Sandpipers in San Francisco Bay estuary. *Auk* 112: 920–930.

Warnock, S.E. & Takekawa, J.Y. 1996. Wintering site fidelity and movement patterns of Western Sandpipers *Calidris mauri* in the San Francisco Bay estuary. *Ibis* 138: 160–167.

Weimerskirch, H., Bonadonna, F., Bailleul, F., Mabille, G., Dell'Omo, G. & Lipp, H.-P. 2002. GPS tracking of foraging albatrosses. *Science* 295: 1259.

Wenstrom, W.P. 1973. Habitat utilization and activities of female American Woodcock *Philohela minor* (Gmelin) in northeastern Minnesota during spring and summer. PhD dissertation, University of Minnesota, Minneapolis.

Wheeler, W.E. 1991. Suture and glue attachment of radio transmitters on ducks. *J. Field Ornith.* 62: 271–278.

White, G.C. & Garrott, R.A. 1990. *Analysis of wildlife radio-tracking data.* Academic Press, San Diego.

White, G.C. 1996. NOREMARK: population estimation from mark-resighting surveys. *Wildlife Soc. Bull.* 24: 50–52.

Whittingham, M.J. 1996. The use of radio telemetry to measure the feeding behavior of breeding European Golden-Plovers. *J. Field Ornith.* 67: 463–470.

Whittingham, M.J., Percival, S.M. & Brown, A.F. 1999a. Notes on night-time activity of Golden Plover *Pluvialis apricaria* chicks in the north Pennines. *Wader Study Group Bull.* 90: 56–58.

Whittingham, M.J., Percival, S.M. & Brown, A.F. 1999b. Evaluation of radiotelemetry methods in measuring habitat choice by young Golden Plover *Pluvialis apricaria* chicks. *Bird Study* 46: 363–368.

Whittingham, M.J., Percival, S.M. & Brown, A.F. 2000. Time budgets and foraging of breeding golden plover *Pluvialis apricaria. J. App. Ecol.* 37: 632–646.

Wood, A.G. 1986. Diurnal and nocturnal territoriality in the Grey Plover at Teesmouth, as revealed by radio-telemetry. *J. Field Ornith.* 57: 213–221.

Yalden, D.W. 1991. Radio-tracking of Golden Plover *Pluvialis apricaria* chicks. *Wader Study Group Bull.* 63: 41–44.