

A CRITICAL REVIEW OF CARTWHEELING FLIGHTS OF RAPTORS

R.E. SIMMONS* & J.M. MENDELSON**

*Ministry of Wildlife, Conservation and Tourism, P/Bag 13306, Windhoek, Namibia.

**P.O. Box 80044, Olympia, Windhoek, Namibia

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Aerial cartwheeling flights of raptors, particularly eagles, are spectacular interactions in which birds lock feet and fall earthward while cartwheeling about a common axis. This is traditionally seen as courtship behaviour, despite the fact that injuries and some fatalities have been reported. We solicited unpublished accounts from 20 raptor biologists world-wide and reviewed published evidence for the courtship interpretation among 39 species of large and small falconiforms. In 82% of 107 cases in which detailed observations were available, whirling flights were aggressive interactions between territorial birds and intruders. Cartwheeling also occurs as play behaviour and as aggression during parent-offspring conflicts. Cartwheeling in Fish Eagles *Haliaeetus vocifer* was confirmed as mainly intra-sexual aggression by T. Liversedge (pers. comm), who induced over 200 cartwheeling events in 5 years by providing fish on territorial pairs' boundaries. Cartwheeling during courtship is described between presumed paired birds in three species of *Haliaeetus* eagles, and one vulture (11% of 107). However, only in one report is unequivocal evidence provided that the birds were paired. We conclude that whirling interactions are mainly aggressive encounters and suggest that observer-expectant bias and other factors may have led to a general misinterpretation of cartwheeling as courtship.

INTRODUCTION

Whirling or cartwheeling flights of large raptors, particularly eagles of the genus *Haliaeetus*, usually involve adults locking feet high above the ground, and falling earthwards. During the descent, the birds whirl in a vertically-oriented plane and usually part before they strike the earth or water below. This spectacular but poorly documented behaviour is frequently referred to as a "display" and an integral part of courtship (Brown & Amadon 1968; Brown 1980; Steyn 1984, 1990). This view has been encapsulated by the well-known 1881 verse of the American poet Walt Whitman, "The Dalliance of the Eagles", which is often cited by popular writers on the subject (e.g. Brown 1980; Love 1983) and taken as implicit evidence (Steyn 1984) for its courtship function. The fact that Whitman never witnessed the "rushing amorous contact high in space together" (Gerrard & Bortolotti 1988) appears not to have dampened the enthusiasm for quoting it.

Despite criticisms (Hansen 1985) and strong evidence (Saunders 1985; Gargett 1990) that whirling or cartwheeling flight is not of courtship significance in African Fish Eagles *Haliaeetus vocifer* or Black Eagles *Aquila verreauxii*, it has become accepted as mainly courtship in the most recent popular raptor literature (e.g. Village 1990a). Here we critically assess the perception that whirling flights of both large and small raptorial birds are usually of pairing, courtship or nuptial significance, by reviewing the literature and unpublished observations on the flights. One should bear in mind that because of the rare occurrence of such interactions much of the reviewed material is anecdotal in nature and from amateur observers.

METHODS

Our literature review encompassed recently published single-species monographs, as well as re-

views (e.g. Newton 1979; Cramp & Simmons 1980; Brown *et al.* 1982; Cade 1982; Steyn 1982; Palmer 1988), published journal papers and more popular accounts. We attempted to extract data on the context of the flight by establishing: (a) the sexes involved; (b) the territorial nature and (c) pre- and post-whirling behaviour of the participants. This proved difficult in most published accounts because few authors reported these details. Therefore, we additionally solicited information from 27 experienced raptor biologists world-wide. We received 20 replies covering 18 species and thousands of hours of observation. Each interaction is described in the respondent's own words to avoid bias. For a quantitative assessment of the frequency, we tabulated the results (except those involving inter-specific encounters) and allotted them to one of five categories: Aggression, Play, Courtship, Uninterpretable and Unknown. We consider Courtship as behaviour associated with reproduction, to occur during times of the year when breeding activity is expected, to involve adult birds of opposite sexes, to advertise reproductive opportunities, to attract potential mates, and/or to help co-ordinate reproductive events between males and females. Where the author gave no interpretation and too few details were available to make a judgment, we recorded it as uninterpretable. If the reference was unavailable to us and we could not critically assess the evidence (because it was mentioned elsewhere) we recorded it as unknown. Where authors recorded "several" incidents we conservatively tabulated these as two events. Over 200 cases of cartwheeling by African Fish Eagles *Haliaeetus vocifer* that were induced have not been included in the tabulated results. We add our own observations from studies of Northern/Hen Harriers *Circus cyaneus*, African Marsh Harriers *C. ranivorus* and Blackshouldered Kites *Elanus caeruleus*, and then address why authors have traditionally interpreted whirling as courtship.

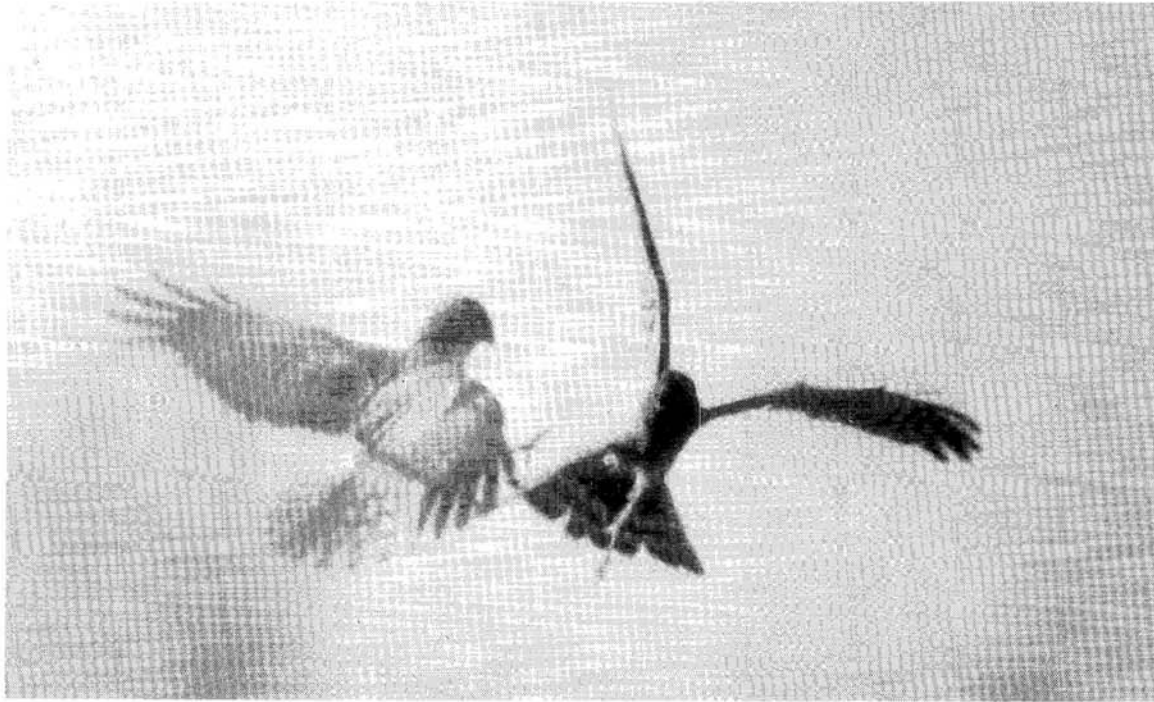


FIGURE 1

An adult male Northern Harrier (left) grasps the feet and talons of an intruding yearling over his nest site, shortly before tumbling to the ground. Intrusions and aggressive responses such as these are relatively common in loosely colonial breeders such as the harriers.

RESULTS

Description of whirling flights

The most quoted source of whirling flight behaviour and evidence for its courtship significance is that of Brown & Amadon (1968: 99). They state: "The pair will be seen soaring over their territory, often calling to one another. The male dives towards the female.... but instead of completing her roll in response, the female grasps his feet firmly with hers. With wings at full stretch, tautly connected by the out-stretched legs, the great birds come tumbling down in a series of cartwheels, over and over one another, often for several hundred feet, finally separating close to the ground or water and flying upwards again". Some variation of this generalised description occurs: some incidents include birds joined only by one foot, others involve talons sunk into the breast and other body parts, some cartwheeling occurs about a horizontal axis and various authors describe whirling birds striking the ground or water at the termination of the encounter (details below). Brown & Amadon (1968) also made no mention (and may have been unaware) of injuries that sometimes resulted from these interactions. We are aware that many reports exist of birds diving at conspecifics, to which the recipients respond by turning in mid air and presenting talons. This behaviour may result in the birds briefly touching without cartwheeling. These interactions

are excluded from our review, but are discussed below. Whirling and cartwheeling or aspects of them are also known as "wheeling", "spinning", "twirling" "talon-linking" or "talon grappling" (Fig. 1).

Incidence of cartwheeling interactions among large species

*African Fish Eagle *Haliaeetus vocifer**

More observations of cartwheeling have been recorded for this species than any other large raptor (Table 1). One of the earliest photographs of grappling birds was that taken by Hutton (1978) of two adults interlocked by their feet and hanging upside down either side of a large branch in the Chobe region of northern Botswana. Their previous history was unknown but on release both were not obviously injured. Remarkably, exactly the same occurrence was photographed in the Okavango region of Botswana, although one adult had sunk its talons into the white breast of the other (Editorial 1984). The observer disentangled the birds and both flew off. Steyn (1984) interpreted this as courtship behaviour with the comment that "neighbouring pairs of eagles maintain their territories by displaying and calling, or flying towards an intruder, and this is usually sufficient to make it give ground without any physical contact".

TABLE 1
A SUMMARY OF THE FREQUENCY OF CARTWHEELING INTERACTIONS AMONG THE WORLD'S FALCONIFORMS. SPECIES BINOMIALS
AND THE SOURCES ARE GIVEN IN THE TEXT

SPECIES	AGGRESSION	PLAY	COURTSHIP	UNINTERPRETABLE	UNKNOWN
African Fish Eagle	9	—	2	2	—
Bald Eagle	6	2	—	—	—
Whitetailed Eagle	3	—	1	—	—
Whitebellied Sea Eagle	2	1	5	1	—
Martial Eagle	2	—	—	—	—
Black Eagle	6	—	—	—	—
Golden Eagle	4	—	—	1	—
Wedgetailed Eagle	2	1	—	2	—
Imperial Eagle	2	—	—	—	—
Tawny Eagle	1	—	—	2	—
Booted Eagle	1	—	—	—	—
Bonelli's Eagle	—	—	—	—	2
Ayre's Hawk Eagle	—	—	—	1	—
Crowned Eagle	1	—	—	1	—
Philippine Eagle	—	—	—	—	1
Bearded Vulture	—	—	4	1	—
Black Vulture	—	—	—	3	—
Egyptian Vulture	—	—	—	—	2
Blackbreasted Buzzard	1	—	—	—	—
Swainson's Hawk	—	—	—	1	—
Augur Buzzard	—	—	—	—	1
Jackal Buzzard	1	—	—	—	—
Common Buzzard	3	—	—	2	2
Redshouldered Hawk	1	—	—	—	—
Blackshouldered Kite	15	—	—	—	—
Peregrine Falcon	2	2	—	—	—
Lanner Falcon	2	—	—	—	—
Aplomado Falcon	1	—	—	—	—
European Kestrel	4	1	—	1	—
Brown Falcon	2	—	—	—	2
African Marsh Harrier	6	—	—	—	—
European Marsh Harrier	2	—	—	—	—
Northern/Hen Harrier	5	—	—	1	—
Australian Marsh Harrier	1	—	—	—	—
European Goshawk	—	—	—	—	1
Eurasian Sparrowhawk	2	—	—	—	1
Red Kite	1	—	—	—	2
Whistling Kite	—	—	—	—	1
Black Kite	—	—	—	—	3
TOTALS	88	7	12	19	18

This view prompted a detailed account of Fish Eagles interacting before and during a whirling flight. Saunders (1985) observed two adults fly "into" one another from opposite banks of the Zambezi River and fall whirling into the water below. After several minutes of flapping one bird struggled out leaving the other alive but floundering in the river. The first bird then dived at and struck the second twice. The observer rescued the floating bird (which was about to be taken by a crocodile) but it died of neck and breast injuries. Steyn (1985) in commenting on this episode conceded that previous accounts of entangled Fish Eagles in Botswana may have resulted from fights!

In his monograph on the Fish Eagle, Brown (1980) states that he observed adult eagles whirling four times during about 20 years of observations in East Africa. Detailed observations for one such interaction are described as follows: "...A pair soaring together suddenly clasped claws and came whirling down in a series of cartwheels till they separated just above the water and mounted to the sky again on thermals. The magnificent aerial performance was actually an advanced form of display, and not a fight, for I had seen the pair do it together". In another event ob-

served in Botswana, Brown observed two birds whirl in a horizontal plane, until they parted just above the water. While we take these two observations at face value as courtship (Table 1), Brown did not describe the post-whirling behaviour, and gave little evidence (other than proximity) as to why he believed the birds were mates.

S. Thomsett (*in litt.*) observed two Fish Eagles over Lake Naivasha, Kenya, calling vociferously shortly before making contact at about 800 ft (246 m). Both birds continued calling as they "violently spiralled straight down". They disentangled at 200 ft (62 m) and one chased the other out of sight over the lake. Thomsett (*in litt.*) regarded the interaction as aggressive.

In Zambia, J. Auburn (*in litt.*) observed two Fish Eagles, talons already locked, tumbling to the ground. They hit the ground, still locked, without apparently injuring themselves, where they fought briefly by lunging with their beaks and feet. In a second incident seen in 1989, Auburn again observed two eagles fly straight at each other over the Luangwa River, Zambia. As they came together, both birds extended their legs and feet, locked together and tumbled about 200 m before hitting the ground. The birds were seen vigorously flapping and calling before parting

5–10 s later. Feathers and disturbed ground at the point of impact suggested they had fought briefly. Auburn (*in litt.*) interpreted both interactions as aggressive.

In August 1985, RES observed three adult Fish Eagles calling while in flight over a lake in South Africa. Two had already locked together and were whirling towards the lake, dropping about 100 m before parting above the water. One immediately started chasing the other across the lake, while the third bird remained soaring overhead; RES interpreted the interaction as an intrusion by an adult into the territory of a known pair, which was then aggressively repelled.

Over Lake Kariba, Zimbabwe, K. Hustler (*in litt.*) reported two birds soaring together. One bird dived at the other which presented talons and they locked together. They spiralled down (distance unstated) and then released with no further interactions. A second interaction was observed between an adult and a juvenile over Lake Kariba. The birds locked together, spiralled "for a while" and released. The adult flew off and the juvenile perched in a tree. Hustler (*in litt.*) offered no interpretation of either interaction, but the involvement of an adult and juvenile in the second observation suggests an interpretation other than courtship.

Bald Eagle *Haliaeetus leucocephalus*

Gerrard & Bortolotti (1988), in the only monograph available to us, cite the incidence of cartwheeling as "occasional" in a long term study of marked birds. They state that it is more commonly an aggressive interaction but present little evidence for that. They have never seen immatures whirling but they do toe-touch, in which case it is probably play (Gerrard & Bortolotti 1988: 54 & 160). Palmer (1988: 208) also describes cartwheeling as "not often witnessed", and provides no references for a generalised description of cartwheeling.

In a 5-year study of Bald Eagles in Florida, P. Bohall Wood (*in litt.*) observed only one cartwheeling interaction: One adult had just caught a fish and was flying with it when a second adult attacked the first and grabbed the fish in its talons. The birds tumbled, cartwheeling through the air and hit the water where they separated. Bohall Wood (*ibid.*) interpreted the cartwheeling as aggression over prey.

During a 6-year study of Bald Eagles by A. Harmata (*in litt.*), whirling was observed on four occasions. All occurred in winter, involved subadult-adult or subadult-subadult interactions and were associated with food carcasses. Some involved piracy attempts, while others involved territorial infringements. Whirling was never seen in a courtship context and Harmata interpreted each event as aggression.

Several interactions apparent between "the sexes and all ages" among over-wintering eagles in the Chilkat valley, Alaska were described by Rearden (1984) as play. Few details were given, but the super-abundant food source of dying sal-

mon, and the season, suggest that food-competition and courtship were unlikely. Pending further details we cautiously concur with Rearden's (1984) interpretation of play, but note that fighting over fish, despite super-abundance, was recorded.

White-tailed Sea Eagle *Haliaeetus albicilla*

In his monograph on the re-introduction of this species, Love (1983) cites three incidents, stating that males "engage and lock talons" aggressively (e.g. Gray 1870 and Fischer 1970 in Love 1983). In one case a bird was injured on impact with the ground, and two other cartwheeling birds fell into a loch. However, Love goes on to describe a generalised display by pairs which cartwheel, following swooping by one bird on the other. During high intensity flights, locked birds tumble out of the sky with feet firmly locked. No specific examples are provided, however. The display has never been seen between immature birds (Love 1983).

White-bellied Sea Eagle *Haliaeetus leucogaster*

Tubb (1978) reported two pairs of sea eagles soaring together over their nest sites in northern Borneo. While two of the birds alarm-called, the two others silently planed directly towards each other some 300–400 ft (92–123 m) above the water. They then thrust their feet forward and simultaneously braked as they made contact, and locked together with their right feet. They subsequently spun down in a horizontal plane, before parting about 20 ft (6 m) from the water. As they circled upwards again, both birds began alarm calling and then repeated the entire performance, before being lost to sight. The author gave no interpretation of the incident but since two pairs were involved and all birds were alarm-calling it was probably an aggressive contact between territorial adults.

Lindgren (1972), commenting on a previous report of a pre-copulatory display, states that courtship in this species can be separated into two phases. The first involves "close parallel flying" between mated pairs during which one bird may dive at the other which "side slips or tips over." Lindgren (1972) describes the second phase in general terms as a "talon clasp" display. Following parallel flights the "lower bird turns upside-down and attempts to grasp the other by its talons. If contact is made, both sets of talons lock together, and the pair plummet to earth, swinging wildly round and round... Twenty feet or so from the ground they separate and resume normal flight." Lindgren (*ibid.*) saw the display four times in one week in Papua New Guinea. Specific details of the interactants were not given, and evidence that they were actually paired adults was lacking. However, we tabulated these observations as courtship (Table 1).

In Tasmania, N. Mooney (*in litt.*) observed two events which appeared to be non-aggressive. Two birds whirling from about 200 m fell to within 20 m of the sea, parted and flew to a look-out perch where they allopreened. Mooney interpreted this as courtship. In another incident, two birds fell

cartwheeling for some 200 m, separated and began circling and soaring, accompanied by an immature. While both events were unaggressive, categorical evidence that they were indeed courting (and not playing, for example) was not given. However, we have recorded the first event as courtship and the second as uninterpretable.

Holland (1984: 103) also describes cartwheeling by a male and female of this species following persistent diving behaviour by the male. The birds clasped feet and cartwheeled four times before parting and flew "straight and hard right out of the area". The observations took place at the height of summer "with no breeding season in sight..." Holland (1984) interpreted it somewhat anthropomorphically as arising from "pure joy". We tabulated it, therefore, as play behaviour (Table 1).

Breeden (1990) observed a territorial female White-bellied Sea Eagle call loudly and fly directly towards an intruder which had just caught a snake. The female flew below the intruder and grabbed at the snake with her feet. They "tumbled through the sky" with only the snake joining them before the intruder departed leaving the female to consume the snake. The behaviour was thus aggression over prey.

One interspecific interaction was recorded by Mooney (*in litt.*) in Tasmania. An adult sea eagle which flew close to the nest of a Wedge-tailed Eagle was immediately attacked by the latter and contact occurred at 100 m. Whirling occurred for 80 m before the sea eagle broke away and flew hard out of the area. The interaction was aggressive.

Martial Eagle *Polemaetus bellicosus*

No published accounts were found that described cartwheeling in this, Africa's largest eagle, but three unpublished observations suggest it may occur. A. Kemp (pers. comm.) has a photograph of two birds locked together in the same manner as described for Fish Eagles, hanging either side of a branch. Further details are lacking. J. Auburn (*in litt.*) describes an interaction between a mated pair in Zambia in which the birds clasped talons and tumbled "very briefly" during pendulum and stooping displays. He stated that this was not cartwheeling behaviour, but interpreted it as one bird protecting itself from the other. S. Thomsett (*in litt.*) described an event in Kenya during which a territorial adult male flew at a perched male intruder from behind. The intruder leapt from the branch and thrust his feet forward to meet the incoming male. They cartwheeled to the ground where they disentangled; the intruder was then pursued out of the territory by the adult male. The event was clearly aggressive.

Black Eagle *Aquila verreauxi*

Gargett's recently published, 20-year study of this species in the granitic Matobo hills of western Zimbabwe provides "several" incidents of whirling. She states (Gargett 1990: 48) that whirling "has never been observed in any but aggressive

contacts between Black Eagles". One such interaction ended in death for one participant following head injuries sustained during whirling (Gargett 1967). Another whirling flight off the coast of Cape Town, South Africa involved two birds maintaining their grip until they hit the sea below, where they would probably have drowned had they not been rescued by the observer (quoted in Steyn 1982).

K. Hustler's observations (*in litt.*) in the Matopos, Zimbabwe confirm Gargett's interpretation. He states that an adult "attacked" a subadult prompting the younger bird to turn over in mid air. They locked together on one leg only and spiralled down to almost tree top height and there separated. The interaction was aggressive.

Of courtship in Black Eagles, Gargett (1990: 45) says: "... the male Black Eagle will fly above the female and (a) sometimes dive shallowly over her with legs partly lowered. She will perform a half-roll beneath him, but they do not make contact". Later (p 46) Gargett states: "No foot-touching, parachuting, or whirling, as described by Brown & Amadon (1968) has been observed in a courtship context". We can conclude that whirling flights for Black Eagles in the Matobo Hills never occur in a courtship context and all such interactions are of an aggressive territorial nature. Thus Broekhuysen's *et al.* (1974) observations of two of six interacting Black Eagles in South Africa, whirling and all but hitting rocks in their descent can probably be ascribed to aggression. The birds parted moments before hitting the ground and their subsequent behaviour was not described.

Golden Eagle *A. chrysaetos*

Whirling flights are apparently seldom observed in this species either in North America or Scotland. J. Watson (*in litt.*), studying Golden Eagles in various parts of Scotland states that he has never seen such behaviour, while D. Ellis (*in litt.*) in North America observed it only twice in a 4-year study. Both cases involved an immature and a territorial adult (Ellis 1979) which clasped talons and whirled for one revolution before the immature birds left the area rapidly. In another incident Ellis (1992) recorded two males, attending a female, who were stooping at each other. After 6 min the two males bound together and whirled at least 19 times, falling about 100m before disappearing below a forest canopy. The two remained grounded, possibly fighting, before they resumed stooping at one another. All interactions were clearly aggressive.

Orton (1974) observed two Golden Eagles in Scotland flying close to one another, before locking together at 150 m and parting out of sight. They returned, flying parallel courses over the moorland, but further details were lacking; no interpretation was given. Two Golden Eagles falling locked together for hundreds of feet in Switzerland (Gilbert 1951) appeared to be a dispute over a hunting territory, but again, details are lacking.

P. Benson (*in litt.*) saw no cartwheeling during a study of Golden Eagles in Idaho but he did find

two young birds electrocuted over power lines with their claws in each other's breasts.

Wedge-tailed Eagle *Aquila audax*

Three observations of cartwheeling flights between Wedge-tailed Eagles are known to us (Debus 1978, N. Mooney *in litt.*). During interactions between a single adult and three intruding immatures, one young bird dived at another which "presented talons". They locked feet and cartwheeled several times before breaking free. Subsequent events were not recorded, but Debus (1978) interpreted the interaction as play behaviour. In Tasmania, an eagle attacked another adult male perched holding a lamb carcass 50 m above the ground (Mooney *in litt.*). The first jumped from the carcass in defence, and the two whirled to the ground where they broke contact and sparred for 10 - 20 s. The first bird then flew off, pursued by the second for 200 m. The interaction was aggression over food. The second event occurred between two adult males which were observed already cartwheeling from 200 m to the ground. Some 25 min later the two birds were found locked by their feet, fighting on the ground. One flew off and the other was caught by the observer (Mooney *in litt.*). The interaction was aggressive.

Other events, for which no details are available, include two fighting eagles which were caught by the observers on the ground and another in which one eagle was killed by the other (Mooney *in litt.*).

Imperial Eagle *A. heliaca*

Only one reference describing aerial contact between conspecifics is known to us. Alonso *et al.* (1987) noted aggressive interlocking of feet between parents and their offspring at the time of independence. Detailed accounts were not provided but the behaviour was seen several times, and coincided with the renewed aerial territorial activity of the adults in autumn. Since the talon-locking led to the departure of the young from the territory it was clearly aggression. A report of "flight play" by cartwheeling Imperial Eagles (Mountfort 1958 in Cramp & Simmons 1980) gives too few details for an interpretation.

Tawny Eagle *A. rapax*

No courtship displays were seen by Steyn (1973) during his observations of Tawny Eagles in Zimbabwe. He states however, "they may occasionally whirl downwards with interlocked claws as described by Brown (1960)". He continues "Bell (*in litt.*) describes such a display in the Kruger Park, and in this case both birds plummeted to the ground before separating." No evidence is given for the context to these interactions. That the latter observation involved birds striking the ground suggests some aggression. An adult male grappling and cartwheeling with its own offspring five weeks after it had left the nest (Steyn 1973) is reminiscent of the parent-offspring aggression in Imperial Eagles (Alonso *et al.* 1987), but too few details are given for an interpretation.

Other cartwheeling events were observed following the chasing by one Tawny Eagle of another holding food in Kenya (S. Thomsett *in litt.*). One bird grabbed the food which brought both birds to the ground from about 20 ft (6 m). This was aggressive piracy.

Wahlberg's Eagles *A. wahlbergi*

J. Auburn (*in litt.*) in a study of this small eagle in Zambia observed no cartwheeling. The only contacts observed occurred when paired males occasionally touched the back of their mates eliciting a roll and presentation of talons. Similarly, no cartwheeling was evident in advertisement displays or fighting during a 4-year study in South Africa (RES pers. obs.). Hence, this is the only well-studied *Aquila* eagle for which cartwheeling is unknown.

Little Eagles *Hieraaetus morphnoides*

Mutual soaring by paired adults sometimes involve "mock attacks" and were seen during a 2-year study of Little Eagles by Debus (1983). Males swept above their mates during aerial flights, causing the female to roll over and present talons. Sometimes both "tumbled about each other briefly" but without making contact. No aggressive contacts were observed during the study in New South Wales (Debus *in litt.*).

Booted Eagles *H. pennatus*

Steyn & Grobler (1981) do not describe cartwheeling flights by breeding African birds. However, they noted that one eagle harassed by a crow, turned in mid-air, grabbed the crow and they tumbled out of sight. Both birds were seen later, and the interaction is best described as aggressive harassment.

Among European populations of Booted Eagles, Jones (1991) described an interaction in September involving seven eagles, some of which were juveniles. Two pale morph adults, a male and a female, locked talons on the male's third dive at the female and cartwheeled an unstated distance before disengaging. Both birds headed off with rapid wing beats and then parted to mix with other eagles. Jones (*ibid.*) noted that this was "intriguing" behaviour for an apparently mated pair. He also stated that "leg-dangling" occurred prior to the display and interpreted this as possibly an "invitation to link talons". However, Barnard & Simmons (1985) have shown that such leg lowering behaviour is more frequently a threat display by territorial raptors than courtship. We interpret the interaction as aggression because (i) it was preceded by leg-lowering, (ii) the pair did not remain together after the cartwheeling and (iii) it took place at the end of the breeding season. Jones (*in litt.*) later also interpreted the event as "largely aggressive".

Bonelli's Eagle *Hieraaetus fasciatus*

While "mutual cartwheeling" is said to be confirmed in this species (Glutz *et al.* 1971), details are lacking.

Bateleur Eagle *Terathopius ecaudatus*

Of 185 intra-specific aggressive interactions recorded during a 4-year study in South Africa (Watson 1989), none involved talon to talon contact. Birds typically presented talons when dived at (no contact), but they were also occasionally hit in the back by the aggressor. The only behaviour clearly associated with courtship or pair-bonding in this species is allopreening or close perching of paired birds (Watson 1988); no aerial courtship is known. Thus cartwheeling is probably very rare in this species.

Crowned Eagle *Stephanoetus coronatus*

Circumstances surrounding a cartwheeling episode were interpreted as aggressive combat by Kalina & Butynski (unpubl. MS). They watched two Crowned Eagles calling and diving at each other, and then cartwheeling for about 3s before parting. In fact, they believe that an adult female, later found nearby and close to death, was injured during intraspecific aerial battle. S. Thomsett (*in litt.*) has witnessed interactions involving foot grabbing and spinning in this species, but further details are lacking.

Egyptian Vulture *Neophron percnopterus*

Cartwheeling by Egyptian Vultures is described as rare (Glutz *et al.* 1971, Perrennou *et al.* 1987 in Levy 1990), but details were not available to us.

Bearded Vulture *Gypaetus barbatus*

Observations of cartwheeling by Bearded Vultures indicate that it occurs in a courtship context. C.J. Brown (*in litt.*) observed 11 pairs over a three year period in Lesotho, southern Africa, and on four occasions marked, paired birds grasped feet and cartwheeled. All cartwheeling was seen in May and June, was initiated by the male (in the nest-building period) and occurred in the nesting area in late afternoon. Prior to cartwheeling both birds dived at each other and some chasing and calling by both birds was seen. As the uppermost bird approached, the lower bird would turn over and present talons. On most occasions talon contact was made and in 30% of such cases the birds cartwheeled for about 200 m. Birds typically parted 100–200 m above the ground and thereafter flew to their nest, side by side, and there roosted or allopreened.

Aggression on the other hand, in this species is manifest in the form of one bird flying alongside the other and hitting it with its stiff outer primaries (Brown *in litt.*). Talon grappling was not observed in any aggressive encounters during the study. Ali & Ripley (1968) (in Cramp & Simmons 1980) describe mutual cartwheeling, following a spectacular flight pursuit, in which the birds parted just meters above the ground. Further details to interpret the interaction were not available.

Black Vulture *Aegypius monachus*

Where several pairs nest close to each other in Europe, aggressive interactions between neigh-

bours "often" escalate into aerial fights including cartwheeling (Meyburg in Cramp & Simmons 1980). The same behaviour has also been seen between pairs which cartwheeled 100 m. Meyburg comments that such fights are easily mistaken for "courtship flight play". In the absence of further details we tabulated these events as uninterpretable (Table 1).

Blackbreasted Buzzard *Hamirostra melanosternon*

Displays for this poorly-studied Australian species have been described recently by Baker-Gabb (1990) who observed a mated male diving at its mate which responded by turning over and touching feet. No cartwheeling was observed, however, and the pair continued soaring. In a second incident, Baker-Gabb described one bird pursuing another with deep purposeful wing beats, before diving twice at the second bird. The latter flipped over and locked claws with its pursuer. They fell in a fast spin for 30 m before disengaging. Since the pursuit was continued, the event was aggressive.

Jackal Buzzard *Buteo rufofuscus*

Only one physical interaction was found for this species. In July 1991, W.R. Tarboton (*in litt.*) observed two adult birds calling in Lesotho, southern Africa, as one bird dived at the other. The lower bird turned, presented talons, and the two fell, locked together for some 10 m before parting and heading in different directions. One joined its mate at a recently completed nest site about 2 km away and the other flew towards a known territory in the opposite direction. The interaction was thus aggressive, probably at a mutual territorial border.

Common Buzzard *Buteo buteo*

In a remarkable incident recorded by Gilbert (1951), two buzzards in Scotland involved in a "fierce fight came hurtling down and landed on the neck of [the] horse [the observer was riding]" in March 1951. The birds survived the fall and the event was clearly aggressive. Two other incidents are described from Wales of buzzards locked together in attempts to drive intruders from known nest sites; details of these events and others reported in Cramp & Simmons (1980) are lacking, however.

Redshouldered Hawk *Buteo lineata*

Kilham (1981) observed two hawks cartwheeling earthwards, talons locked together in Florida, and believed both birds were males. The interaction was thus probably territorial and aggressive.

Whirling interactions among smaller raptors

Some 15 cases of whirling interactions have been recorded for Blackshouldered Kites *Elanus caeruleus*. Whirling has been reported from both North America and Africa by Watson (1940), Waian (1974), Bamman (1975), Wright (1978),

Mendelsohn (1981) and Henry (1983). In each case the interaction was described as agonistic. In three examples the birds fell to the ground, and once two birds remained grappling for about 15 s. This species exhibits a variety of high intensity aggression associated with territorial defence and cartwheeling occurs during particularly intense aerial battles. All such battles in South Africa were between neighbours; nomadic intruders were always expelled with lower intensity threats (Mendelsohn 1981).

Cade (1982) reports that talon locking between falcons is not as common as between eagles. He states that "When one mate stoops at the other, the latter often rolls over and presents its talons, and occasionally paired falcons lock talons briefly in these encounters..." True cartwheeling is reported only in aggressive encounters. For example Ratcliffe (1980:202), citing Cade's (1960) description of territorial Alaskan Peregrines *Falco peregrinus*, states "... but quite often the two falcons grapple with each other's talons and, thus locked together, may fall through the air until they almost hit the ground before breaking apart. Occasionally the intruder is actually thrown to the ground... and Cade has seen the intruder pinned on its back... by the rightful occupant". Sherrod (1983) reports aggressive interactions between parents and offspring in which young birds bind to prey carried by the adult and are carried in that fashion, upside down, until the prey is released. During higher intensity interactions of "mock combat" (p 42) young "sometimes" grasp each other's feet and tumble several meters before parting. This we tabulated as play (Table 1).

Sibling Lanner Falcons *F. biarmicus* were observed by S. Thomsett (*in litt.*) in Kenya to "whirl" to the ground (distance not stated) where they fought over food grasped by one of them. The interaction was thus aggressive. In February 1991, in Lesotho, southern Africa, D. Allan (*in litt.*) observed a pair of Lanner Falcons fly out from their cliff site where the male attacked an intruding male. The birds clasped talons and fell whirling, at least 30 m before being lost to sight. Since the attacker was already paired and the event took place well outside the breeding season (March), the behaviour was aggressive.

Australian Brown Falcons *F. berigora* have twice been observed whirling in Tasmania (Mooney *in litt.*). The first incident occurred between two males which made contact at 20m and whirled to within 2 m of the ground. There they broke apart and one bird was pursued by the other while alarm chittering. The second interaction occurred following pursuit between two pairs. The two males made contact at 100 m and grappled while falling until they hit overhead power lines. One bird was decapitated and the other broke both wings in the impact. Both events were aggressive territoriality.

European Kestrels *F. tinnunculus* have been observed on at least two occasions grappling while falling earthward locked together. I. Newton (*in litt.*) interpreted the behaviour as aggressive since it involved two males, and in one instance they

crashed to the ground and continued battling. In June 1955, Suffern (1956) observed a male and female kestrel fly together to about 30 m, grip talons and with "wings held motionless", and the male upper most, "twirl" to grass level before parting. They resumed hunting together. Suffern interpreted the behaviour as play because no aggression was apparent and the birds resumed typical behaviour thereafter. It also occurred during or just after the breeding season. However, these may not have been a mated pair, since Village (1990b) states, in the context of kestrel ranges during autumn and winter, that "I several times saw juveniles that had been hunting close together suddenly start to fight, usually because one bird dived at the other. Such fights could be very aggressive, with the combatants tumbling to the ground and grappling with their talons. The birds would eventually separate, sometimes to resume hunting in the same place as if nothing had happened".

In a filmed sequence, D. Ellis (1992) recorded a young female Aplomado Falcon *Falco septentionalis* diving at a perched, adult male. The latter sprang into the air, grasped the female's foot and whirled one revolution before separating. Ellis (*in litt.*) regarded the interaction as aggressive.

Among African Marsh Harriers *Circus ranivorus*, aerial interactions in which two birds locked together and fell earthwards were seen six times in 2200 h observation in South Africa (Simmons 1991). In one case two females fighting over a territory locked and fell 20 m, before re-appearing 1.5 min later to resume their territorial contest. A second case involved a male defending his flying young from attack by a neighbouring male; the adults fell 3 m locked together at a mutual boundary and remained on the ground for 7 min. The neighbouring male reappeared first and once again struck the youngster, sending it to the ground. This latter behaviour was seen on four further occasions. A third event occurred when a nomadic harrier flew over an active nest and the breeding female flew behind and below the intruder to pull it earthward from about 10 m. They remained grounded for 7 min before the intruder flew swiftly away escorted by the female. The remaining three interactions occurred between a brood of flying young and adult, neighbouring males and females. In these cases, the grappling adults and juveniles fell to the ground, locked together. Each event was accompanied by extreme aggression, including one occasion when an adult male continued diving and attempting to strike a young harrier for 7.5 min, having spent 3.5 min grappling with it on the ground. The young bird survived. Paired birds (patagially tagged) were never seen to cartwheel, or even lock together, during mutual soaring or inter-territorial interactions. Hence all talon-locking interactions in these harriers were aggressive.

Among Australasian Marsh Harriers *C. approximans*, similar incidents involving adult and immature birds have been seen. D. Baker-Gabb (*in litt.*) observed a marked adult male stoop at an immature harrier which flipped over and locked

claws. They tumbled about 10 m before disengaging. Since the immature fled the territory, the incident was territorial aggression. In an inter-specific interaction recorded in Tasmania, N. Mooney (*in litt.*) observed a breeding female Brown Falcon attack a female Marsh Harrier, foraging close to the falcon nest. The two grappled from 30 m to 2 m, where they broke apart and parted company.

Cramp & Simmons (1980) report that cartwheeling among European Marsh Harriers *C. aeruginosus* occurs between two polygynous females when they fly towards a prey-carrying, bigamous male. They lock talons and fall into the reeds. Such events are clearly aggressive. In a similar interaction in Canada, two close-nesting polygynous, female Northern/Hen Harriers *C. cyaneus* locked talons in the early breeding season, following intense leg-lowering interactions, and fell together into a drainage ditch (RES pers. obs.). The polygynous male flew overhead but did not interact. The two females were not resighted for at least 10 min. This was aggressive female-female territoriality. In the same study in April 1980, a foraging female nearing the nest of another, was attacked by the breeding female (RES pers. obs.). The two locked talons over a small copse of trees and fell about 10 m to the ground. They were not resighted. This was aggressive territoriality. Details of two males interacting and grasping feet (in Watson 1977) were not given. Craig *et al.* (1982) reported three instances of cartwheeling by Northern Harriers. In each case the falling birds fell to the ground where, in two cases, they continued grappling, thrashing about and flapping their wings. The three events were interpreted as agonistic behaviour.

Among Scottish Hen Harriers one interspecific interaction occurred with a prey-carrying Kestrel in which birds were seen to tumble "tightly locked together" to the ground, fighting over prey (Watson 1977: 93). Similarly in Canada, in May 1980, a Northern Harrier and Short-eared Owl *Asio flammeus* locked talons after persistent diving by both birds near their nest sites and fell 20 m (owl uppermost) interlocked to the ground. They remained there for 2s before separating (RES pers. obs.).

European Sparrowhawks *Accipiter nisus* have twice been observed by I. Newton (*in litt.*) to clasp feet in mid air and fall earthward. The encounters involved females and followed advertisement displays. Newton interpreted the encounters as aggressive since they involved birds of the same sex. Dawson (1978 in Newton 1986) reports a male and female cartwheeling but details are lacking. Newton (1986) noted that the courtship interpretation given may have been unjustified.

Condry (1974) saw two pairs of Red Kites *Milvus milvus* in Wales in March 1973 flying close to one another above their nest sites. Following much swooping chasing and calling, two birds flew at each other, locked claws and spun earthward. The incident was repeated following separation. During the descent, the whirling birds almost collided with trees and the ground. No interpretation was given, but since two pairs were involved near their nesting area, we suggest it was territorial ag-

gression. Further references in Cramp & Simmons (1980) describing cartwheeling as mainly aggressive, were unavailable to us.

Among Black Kites *Milvus migrans* talon grasping is said to develop into a "cartwheeling ritual" (references in Cramp & Simmons 1980) but details are lacking. Further, a somewhat far-fetched interpretation of cartwheeling between presumed mates was suggested by T. Blanc (in Cramp & Simmons 1980) who reported that males invite females to choose a nest site by cartwheeling with them over the site!

Despite intensive studies on large numbers of individuals, Ospreys *Pandion haliaetus* have apparently never been observed in such activities (Poole 1989).

Additional species observed whirling

Other raptors observed in whirling flights include Swainson's Hawks *Buteo swainsonii* in North America (D. Ellis *in litt.*), Philippines Eagle *Pithecophaga jefferyi* (R. Krupa *in litt.*), Whistling Kites *Haliastur sphenurus* in Australia (D. Baker-Gabb *in litt.*), and European Goshawks *Accipiter gentilis* (Cramp & Simmons 1980) but details are lacking. In Africa, S. Thomsett (*in litt.*) has observed intraspecific interactions involving foot grabbing and spinning among Ayre's Hawk Eagles *Hieraeetus ayresii*, and Augur Buzzards *Buteo augur*, but specific details are lacking. While seen between mated pairs, Thomsett described the brief spinning as "high intensity mistakes" following excited diving at the male by the female. Hence these interactions could not be ascribed to courtship.

Experimental evidence

On completion of this survey, T. Liversedge kindly made known to us a natural experiment with African Fish Eagles which strongly supports our findings. During visits to 15 contiguous pairs of eagles in the pan handle area of the Okavango Swamps, Botswana, Liversedge induced aggressive whirling flights in adjacent pairs by throwing a dead fish into the boundary area between two territories. As the fish drifted into one territory, the presumed male of the territory flew down to intercept it. This action invariably induced the neighbouring male to either attempt to pirate the fish, or to fly towards the prey-carrying male and then back into its own territory. The females of both pairs, however, would take flight, calling and soaring over the mutual boundary, before flying at each other about 30 m above ground, clasp talons and cartwheeling down. They broke apart a few metres above the ground in about 90% of all cases, but hit the water or reeds in the remaining cases, still entangled. Liversedge (pers. comm.) induced this behaviour at least 200 times in about five years and knows of one fatality during that period. Commenting on possible courtship, Liversedge states that known mated pairs do rarely cartwheel, but only briefly (2-3 revolutions) and without ever falling the distance seen among territorial cartwheeling birds. These observations and natural experiments, albeit fortuitous, support the

idea that cartwheeling is principally aggressive during intra-sexual contests in Fish Eagles.

DISCUSSION

Of 39 species of birds of prey, ranging from small falcons to the largest eagles and vultures, detailed observations of 107 cartwheeling events are available for 29 species (Table 1). Of these, 82% involved aggressive interactions, either territorial in nature, food piracy, defence of young or parent-offspring conflict. Seven interactions (7%) were interpreted as play. Only five reports, involving 12 (11%) interactions, give descriptions of cartwheeling as courtship behaviour (Brown 1980; Love 1983; Lindgren 1972; C.J. Brown *in litt.*; N. Mooney *in litt.*)

Biases and interpretations

Almost without exception we observe the following dichotomy: in **generalised** accounts of whirling interactions the author(s) interpret the behaviour as a display with courtship significance, while in all but two **specific** accounts (mainly unpublished observations) the observers provided evidence that the interactions were aggressive. The large number of unpublished accounts with an interpretation of aggression suggests the observers may have been discouraged from publishing them because they went against the grain of accepted "truths". For example, nine examples of aggressive cartwheeling among African Fish Eagles were found, only three of which were published (two of which were misinterpreted). For accounts that were published in which aggression occurred, authors were noncommittal. For example, Jones (1991) describing Booted Eagles interlocking was "intrigued" by the behaviour following the interaction probably because the dyad did not act as a mated pair. We suggest that previous interpretations and warnings against mistaking whirling as fighting (Brown & Amadon 1968 quoted below, Brown 1980) may have discouraged authors from publishing altogether or influenced them to interpret all displays uncritically as courtship. This type of observer-expectant bias is apparently common in ornithology, although subtle and rarely appreciated, particularly in behavioural studies (Balph & Balph 1983; Balph & Romsberg 1986).

The main proponent of cartwheeling as courtship seems to have been L.H. Brown (Brown 1976; Brown & Amadon 1968; Brown 1980) who discusses only in passing (Brown & Amadon 1968: 100) the alternative that aggression may be involved. For example, in concluding their chapter on aerial displays of raptors, Brown & Amadon (1968) state: "The main possible error to avoid seems to be mistaking display for fighting. It is generally safe to assume that when two large raptors are seen apparently battling far overhead they are not fighting, but are a mated pair indulging in mutual display".

Judging from the independent reports (above) of aggressive interactions concerning one of Brown's main study species, the African Fish Ea-

gle, it seems likely that either (i) Brown misinterpreted the behaviour, and subsequently over-extrapolated his views of whirling Fish Eagles to all large species (quote above) or (ii) interpreted correctly, but disregarded other reports of birds obviously fighting or falling into the sea still entwined as exceptions (e.g. Brown & Amadon 1968: 100). For example, even his monograph on the Fish Eagle (Brown 1980) includes a photograph (by T. Liversedge) of an adult pair of eagles whirling while fighting over a fish held by one combatant. No mention is made of this incident in the text. That some fatalities are known (Newton 1979; Gargett 1990) and were published prior to 1968 (e.g. Gordon 1955) on a species (the Golden Eagle) he studied (e.g. Brown & Watson 1964), make Brown's views puzzling. That other authors have uncritically followed Brown's interpretations may be due to the observer-expectant bias described as follows by Balph & Balph (1983) "... if one author is perceived as a confident, authoritarian figure, observers are more likely to bias observations in the direction of the researcher's expectancies than if the researcher is not such a figure." We conjecture this has occurred frequently with interpretations of whirling flights.

Authors who interpreted cartwheeling as courtship may have also been influenced by the similarity between the incipient stages of courtship and cartwheeling. It is well known (e.g. Brown & Amadon 1968; Debus 1983; Gargett 1990 quoted above) that males do indeed dive at their mates, sometimes with legs extended and pass close enough to them to cause the female to turn in mid-air and present their open talons. Several authors noted this to the extent that mates briefly touched feet or rolled around each other without touching (e.g. Debus 1983). Others believe that males become highly excited during such interactions and females may be forced to defend themselves as the males' passes become closer and more intense (Thomsett, above; Cade 1982). That this can be seen as a logical extension of a courtship sequence (e.g. Brown 1976; Lindgren 1972) which evolves into cartwheeling is easy to see, but we believe is probably incorrect.

An additional reason for misinterpretations of whirling flights, even by experienced raptor biologists, is that the birds usually involved are sexually monochromatic and unsexable in the field. This is true for the African Fish Eagle, the White-bellied Sea Eagle, and the White-tailed Sea Eagle—those species most often quoted as whirling during courtship. We also note that Brown's (1980) observations were of dense breeding Fish Eagle populations in which one might expect more aggressive interactions than courtship, particularly in a species which possibly pairs for life (*ibid.*). Furthermore, Brown's (1976) main justification that whirling is courtship came from the observation that the pairs observed cartwheeling were circling together shortly before cartwheeling occurred. Even this is equivocal evidence since territorial interactions in a marked population of the similarly monochromatic Bald Eagle are described by Gerrard & Bortolotti (1988) as follows:

"Sometimes interlopers casually soar across a territory and are silently escorted away by a member of the breeding pair. If you hadn't kept close track of who was who, you might think that the two birds soaring together were the residents". We thus conclude that it is easy to mistake whirling as courtship because (i) of observer expectant bias; (ii) aspects of courtship or play suggest a natural progression to whirling; (iii) many raptors are difficult to sex in the field, and (iv) birds soaring together are not necessarily paired.

The function of cartwheeling

Among various accounts of whirling it appears that some birds, particularly larger ones, do not appear to grapple during the interaction but extend their legs to the full extent. This is unexpected if the whirling is primarily an extreme form of territorial aggression. Since many flights end just before the observers expected the participants to strike the ground, we speculate that one purpose of the interaction might be for the aggressor to drive the intruder into the ground. Hence the whirling may evolve from the constant shifting of each bird in its attempt to regain the upper dominant position. That female African Marsh Harriers (RES pers. obs.) and Peregrine Falcons (Ratcliffe 1980) indeed fly below intruders and drag them earthwards before righting themselves just before impact, supports this scenario. Indeed, that cartwheeling in species such as Wedgetailed Eagles, Golden Eagles, Black Eagles, African Fish Eagles and Brown Falcons has resulted in death for one combatant, reflects the extreme aggression inherent in such encounters.

It is of interest to note that each time aerial flights of raptors (which are not migrating or foraging) have been subjected to critical re-examination, such as here, aggression or some form of territoriality has been suggested as the primary motivation. For example, Harmata (1982) re-examining the presumed sexually-motivated undulating flights in Golden Eagles, concluded it was principally territorial in nature. Collopy & Edwards (1989) in an independent assessment of the same species concurred with this interpretation. Iribarren (1975) in a study of the Booted Eagle suggested that all three major flight patterns were territorial and not courtship in function, while Watson (1988) found no evidence for courtship flights in the highly aerial Bateleur. Similarly, Barnard & Simmons (1985) concluded that aerial leg-lowering by raptors in southern Africa were primarily threat displays, and Mendelsohn (1981) reported that "shallow flapping" displays of Black-shouldered Kites occurred both in territorial disputes and nest site displays. However, that some such flights should be seen as "advertisement" displays and not exclusively territorial was apparent in the skydancing displays of two species of harrier which have a mate attraction component (Simmons 1988, Simmons 1991). Likewise "rocking flights" by Kestrels may seem to have a courtship function because they are often performed by pairs in spring, but Village (1990b) suggests that they are used mainly in terri-

tory defence and advertisement. Newton (1986) concludes similarly for European Sparrowhawks. Nevertheless, since raptors are rarely vocal, have good powers of flight and cartwheeling interactions are here shown to be mainly aggression, we suggest that many raptor flights, other than migration or foraging, may represent territoriality and less often courtship or mate-attraction.

CONCLUSIONS

We have now come full circle: we conclude from this first review of published and unpublished accounts of cartwheeling interactions, that it is unwise to assume that any raptors observed in such flights are courting (*contra* Brown & Amadon 1968). Instead we have shown that such interactions are more typically (i) fights over a territory or food; (ii) aggressive interactions between parents and offspring or (iii) play behaviour of immatures. Unequivocal evidence for a courtship function is given only for colour-marked Bearded Vultures and is lacking in other species because the identity of participants in whirling events is seldom given. While our review has shown that most interactions are not courtship, we do not claim that whirling of short duration will never be shown to be of nuptial significance. However, many more details on sex-identification, and post-whirling behaviour need to be provided in such reports. While we also suggest that many aerial flights of raptors, previously assumed to be sexually-motivated, are instead mainly territorial, a clearer understanding of the aerial behaviour of mated pairs is required. Such an understanding should aim to distinguish between elements of courtship, play and aggression.

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