Territories and local movements of African Black Ducks

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Introduction

The African Black Duck *Anas sparsa* lives almost exclusively on rivers and, like the few other duck species which are year-round river specialists Salvadori's Duck *Anas waigiuensis*, Torrent Duck *Merganetta armata*, and Blue Duck *Hymenolaimus malacorhynchos*, breeding pairs are believed to be strongly territorial. The aim of this paper is to document the territorial behaviour of individually marked African Black Ducks and to report on their local movements and activity patterns.

The study was begun in January 1972 (by WRS and PGHF) when several birds were colour-marked on the Eerste River near Stellenbosch, South Africa. The wariness of the birds made them difficult to approach, however, and they were often hard to observe because of trees and other obstacles. In March 1973, the study was intensified to include radio-tracking of the birds and observations from blinds built at strategic points along the river. Most results reported here are from the intensive study period (March 1973 to June 1974) when all four of us worked on the project. Less intensive tracking and observations (by WRS and PGHF) from July 1974 to February 1976 have extended our knowledge of the long-term history of a number of birds.

Study areas

Most of the tracking and observation effort was concentrated along a 3·4 km stretch of the Eerste River just below the town of Stellenbosch. When marked birds moved outside this core area, we searched for them on more distant parts of the Eerste River, on the tributary Blaauwklip River, and on irrigation dams which are common in the area (Siegfried *et al.* 1975). Except for 10–100 m bands of relatively undisturbed wooded habitat along the rivers, the Eerste River Valley is intensively cultivated. Most of the large trees remaining along the rivers are exotics, including several species of Australian acacia *Acacia melanoxylon* and *A. longifolia* and oak *Quercus robur*.

The Eerste River Valley is located in the austral winter rainfall region. The wet season (usually April through September) begins with spates that scour the rivers and remove much of the silt and debris which has accumulated over the past year. Within a few days the river subsides to within its banks, but generally retains at least moderate depths and flow rates until about November. During the dry summer months, water levels in rivers of the south-western Cape drop, and this is accentuated in the Eerste River Valley by agricultural and other demands upon water supplies. At the peak of the dry season the Eerste River may be reduced to a series of almost stagnant pools connected by rocky stream bed with little or no water. Pools comprise about 30% of the Eerste, and sections of up to 200 m may be of little use to Black Ducks in a dry year. Sand and silt, or bedrock form the substrate of the pools, and the riffles and rapids are underlain by rounded cobbles and boulders. Numerous boulders break the water surface except when water levels are very high. Tangles of brush and debris form during the spates, and banks are often undercut by the current.

In an attempt to relate Black Duck population densities to varying ecological conditions, we censused ducks on the Klein Berg River 80 km to the north, and on the Klipplaat River, 760 km to the north-east of Stellenbosch. We also radio-tracked and intensively observed four Black Ducks on the Klipplaat River for ten days in August 1973. Locations and ecological descriptions of each of the rivers studied are given in Table 2 (p. 74).

Methods

Black Ducks were trapped in mist nets stretched across rivers at strategic points where overstorey prevented ducks from flying over the net. The nets were tended continually to prevent possible injury to trapped birds. Mist nets were less effective on dams than on rivers, because the ducks could often see the net and had more room to manoeuvre and avoid being caught. Most captures at dams were made at night using a 'V' of large mist nets at one corner of the dam. We guided birds toward the nets by making a noise at the opposite side of the dam, and then flushed them with spot lights. One bird was captured at a dam in a floating wire trap containing a captive pair of Black Ducks.

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Birds were weighed and examined for signs of moult or injury each time they were captured. All birds were marked with a metal leg band, and in addition, some were marked with either coloured plastic leg bands, numbered plastic nasal saddles, radio transmitters, or a combination of these marking devices. The radio package consisted of the battery/transmitter module (2·8 × 1·3 × 1·3 cm), a plastic coated flexible wire body loop antenna 32 cm in circumference, and an adjustable, soft plastic neck loop (Figure 1). The coloured soft vinyl back tag (1·2 × 8 cm) was usually visible only when the bird flew. Most of the battery and all of the transmitter and harness components were covered by feathers once the bird had opportunity to preen around the package. Total package weight was 25 g, about 2–3% of adult Black Duck body weight. Battery life averaged approximately 70 days, so key radio-marked birds had to be recaptured about every two months. Retrapping to replace transmitters was relatively easy, since tracking revealed movement patterns and favoured pools. Radio-marked Black Ducks preened relatively more than unmarked birds (Siegfried *et al.* 1977a), but the transmitters caused no apparent behavioural abnormalities which could materially affect the results of our studies.

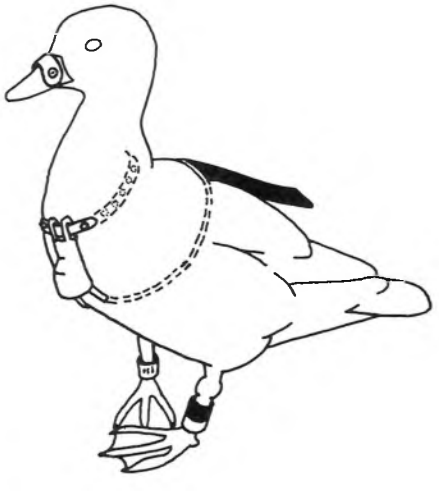

Figure 1. Method of attachment of radio transmitter to an African Black Duck. The backtag is normally visible only when the bird flies. All parts of the harness and most of the transmitter/battery package are normally covered by feathers. The flexible body loop functions as the transmitting antenna. Nasal saddles and coloured leg bands were used on some birds.

Tracking was done with a portable receiver and attached directional loop antenna. A farm road paralleling the Eerste River was marked with numbered stakes at 25 m intervals for reference points. We were able to locate radio-marked birds to within 10 m or less. Each location was assigned to a 10 m × 10 m grid square described by an X–Y coordinate system superimposed on a 1:10,000 air photo map of the area.

When radio-marked birds moved around, as in feeding and bathing, the transmitter antenna loop was flexed and its transmitting plane varied, so that signal intensity and tone changed. Each time a location was determined, the signal was monitored for 30 seconds and any audible changes in signal were recorded. Thus we were able to tell where each bird was, and also whether or not it was active. Each time a radio-marked bird was located, we recorded time, location, and activity. When birds were seen, details on behaviour were also recorded. In addition to making descriptive field notes, we recorded each observation in a coded format for automatic data processing.

Twelve blinds were constructed along the Eerste at places frequented by radio-marked birds. By using these blinds we were often able to observe behaviour and interactions between birds once we had established their locations by radio tracking.

A rigid tracking schedule was maintained from March 1973 to June 1974; we worked in shifts each Tuesday from at least one hour before sunrise until at least one hour after sunset, locating each radio-marked bird about once per hour. Events such as egg laying, incubation, and brood movements were investigated during shorter but more intensive tracking sessions on other days. Tracking of birds away from the study area core was conducted intermittently, as was night-time tracking. Since June 1974, tracking has been continued on a sporadic basis to provide longer-term data on pair bond duration, home range stability, longevity, and breeding success.

Because spacing patterns of some territorial birds are known to be affected by the distance at which neighbouring individuals can see one another, we devised a crude method for determining differences in visibility along the rivers studied. At ten random points along each river, we measured the upstream and downstream distances at which an observer, standing at midstream with his eyes 25 cm above water level, could see a black wooden block (30 × 15 × 15 cm)

anchored in mid-stream perpendicular to stream flow. The mean of the resulting 20 measurements was used as an index of visibility on the river in question. Black Ducks were censused using techniques described by Siegfried *et al.* (1975).

In an attempt to learn more about Black Duck densities on streams other than the four studied directly, we distributed a questionnaire to biologists in South Africa known to be working along streams which might support Black Ducks. We requested information on stream location, size, ecological characteristics, density of Black Duck pairs, and a subjective estimate of census precision (based on number of counts and length of river segment studied).

Results

Since the beginning of the study, 114 Black Ducks have been captured and banded in the Eerste River Valley, many of them several times (180 recaptures). Thirty-two of the birds were radio-marked, and 68 were colour marked only. By 15th June 1974, 10,122 locations of known-identity birds had been recorded, along with approximately 1,500 observations of unmarked birds. During the ten days on the Klipplaat River, we radio-marked five Black Ducks and successfully tracked four of them. A total of 213 locations of radio-marked birds and 31 observations of unmarked birds were recorded.

Territories

Detailed accounts of the social behaviour involved in territorial encounters of Black Ducks are presented by McKinney *et al.* (in press). A brief summary of territorial behaviour is given here, followed by an analysis of the resultant spacing patterns.

Territorial Black Ducks react aggressively toward potential rivals whenever they are encountered in the territory. Each member of the territorial pair typically confronts, and may battle with, intruders of its own sex. Black Ducks usually visit each part of their territory at least once every day, and during periods of intensive pressure from intruders, territorial birds have been seen actively searching places where an intruder might hide.

Territories of Black Duck pairs on the Eerste River averaged about 700 m in length and, except when mate changes or territory takeovers were occurring, two adjacent territorial pairs never shared more than 10% of their combined territory length. Usually, the overlap zone was considerably less; even considering overlaps from pairs on *both* sides, our most intensively tracked pair (F06/M04) allowed a monthly average of only 10·4% overlap, i.e. 89·6% of their territory was totally unused by their neighbours. Overlap zones were not shared peacefully by neighbouring pairs: any intrusion was challenged if detected and challenges were normally successful. Thus, Siegfried's (1968) impression of a '... neat, well defined pattern of exclusive territories ...' is generally supported, although several instances of considerable overlap were documented.

Monthly ranges of six females occupying adjacent territories on the Eerste River are plotted in Figure 2, and these parallel closely the ranges of the pairs involved. The most substantial overlap shown involves F07, and represents an infiltration and eventual takeover of the territory centred around river km 0·5. Female 07 was first captured in June 1972 near river km 0·7 and she was recaptured nearby in March 1973 and equipped with a radio. For several months, F07 was seldom seen, even though her presence could be detected via the radio signal. She spent much of the day in brush piles or in a small irrigation ditch which entered the river near the boundary between the territories of F03/M02 and F06/M04. She was often displaced from the river by the territorial pairs. Like most other non-territorial Black Ducks in the area, F07 left the river each day at dusk and flew to Groote Zalze Dam where many Black Ducks gathered to interact socially and to roost (Siegfried *et al.* 1977b). This furtive existence continued until July 1973, when she was first seen on the river with a male: she had begun the transition from a non-territorial, lone female to a member of a territorial pair.

Little progress was made in usurping territory from the adjacent pair upstream (F06/M04). That territorial boundary remained quite stable and little overlap occurred except during a 'liaison' (a part-time pair bond) between F07/M04 during January 1974 (Figures 2 and 4). Considerable progress was made against the downstream adjacent pair F03/M02, however, beginning with about 15% overlap in August 1973. Male 02 disappeared (injured) on 16th August and a complex series of mate changes took place (see McKinney *et al.* in press, and Figure 4). By March 1974, F07 and her mate had taken over the territory completely and F03 was forced to lead a furtive life when she was on the river. Eventual-

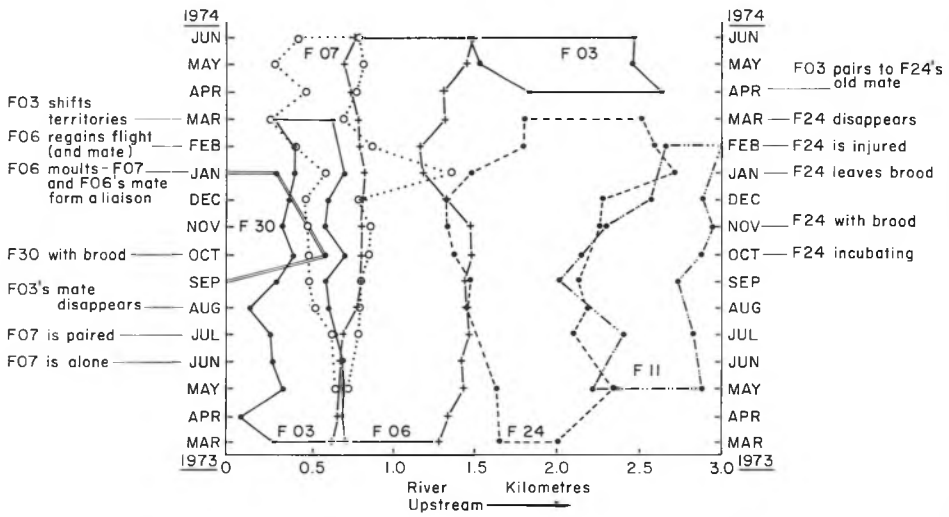

Figure 2. Spatial relationships among six territorial female Black Ducks along the Eerste River. Distances shown are along the river course. Territory boundaries are based on at least 60 locations per month for females 03, 07, 06 and 24, and at least 10 locations per month for females 30 and 11 (total locations = 4,645). Isolated locations (more than 50 m from next nearest locations recorded for the month) and locations of birds in flight were deleted.

ly (April 1974), F03 abandoned the territory entirely and formed a long-lasting pair bond with M08 who had remained on his territory after his previous mate (F24) disappeared about 1st April. Thus the most prominent overlap shown in Figure 2 represents a protracted but eventually complete takeover of a territory, rather than permanent overlap of territories.

A previously mentioned instance of considerable overlap occurred at km 0·8 to 1·2 during January 1974 (Figure 2). During this time M20 and F06 were in wing moult and their mates formed a liaison, behaving much as a mated pair. 'Pair' F07/M04 utilized much of the area previously used by each as members of separate neighbouring territorial pairs. During the wing moult F06 was restricted to a deep pool near the centre of the territory and F07 avoided this area completely. M04 visited F06 in this area daily and on at least two occasions he spent the night there with her. F06 rejoined her mate and they resumed exclusive use of their old territory within two days after she regained flight capability.

Females with broods showed a rather surprising tendency to trespass persistently, though brood rearing occurred primarily on the parents' territory. During October and November, F30 and her brood of five ducklings penetrated upstream to km 0·6, completely passed pair F03/M50, and were finally rebuffed by pair F07/M20 after about a week of aggressive interactions (Figure 2). Note that, at this time, F03 was under considerable encroachment pressure also from F07/M20. Furthermore, she had lost her long-term mate about a month earlier and was newly paired to M50. Since close cooperation between mates appears to be very important in territorial defence (McKinney *et al.* in press), the newness of F03's pair-bond may have been a factor in explaining the extent of the encroachment.

F24 and her brood also persisted in using a contested section of river (km 1·3 to 1·5, Figure 2) during October and November. Use of this segment occurred in spite of frequent confrontations with downstream pair F06/M04. While they lacked the intensity and duration characteristic of attempted territory takeovers during the pre-breeding period, intrusions by hens with broods were nonetheless quite persistent. Well-established territorial pairs generally seemed able to turn back intruding brood females once they were detected, but perserverance by females and broods still resulted in almost daily use of some contested segments of river. It was not usually clear whether trespass during brood rearing was initiated by the female or by the ducklings. Females often swam behind the foraging ducklings and usually made no apparent attempts to lead them back unless the residents were encountered. We saw no

evidence that ducklings recognized or respected territorial boundaries. Only two females (F30 and F24) produced broods during the intensive study period; territorial conflicts would apparently have been even more severe had other females been rearing broods concurrently.

None of the territorial pairs studied on the Eerste River emigrated during the dry season and none established temporary breeding territories during the wet season. Siegfried (1968) suspected that seasonal residence was the rule on the Blaaukwlip River, a shallow tributary to the Eerste. Our data from the Blaauwklip are inconclusive due to sporadic tracking there, but census data presented by Siegfried *et al.* (1975) for 5·38 km of this river do not support the idea of only seasonal occupancy by the majority of Blaauwklip River pairs. The section of river studied in 1968 is farther upstream than the sections we studied, and few pools remain during the dry season. The seasonal residence pattern of Black Ducks on ephemeral streams needs further study.

Note in Figure 2 that the territory arrangement of April 1974 was very similar to that of April 1973; at both times there were three territories in similar locations on the central section of the river, even though several of the inhabitants had changed. The territory centred at km 0·5 remained a relatively small one in spite of a complete change in occupants, while the territory at km 1·9 remained relatively large, even after the resident female changed. Factors which could cause territories to remain stable in size and/or location despite changes in occupants may include: (1) influence of the territorial mate which remains, (2) influence of the adjacent territorial pairs which tend to maintain or expand their territories regardless of the identity of their neighbours, and (3) characteristics of the river segment itself such as availability of suitable sites for feeding, roosting and moulting.

While one might expect that territory boundaries would be situated in relation to topographical features of the river, no such tendency was recognized. Territory boundaries occurred where bends in the river or obstructions provided a sight barrier and also where visibility was relatively unrestricted. Some were situated at favoured feeding pools while others bisected river segments with low potential as feeding sites.

Pair bonds

A representative example of the very close spatial ties between mated territorial Black Ducks is shown in Figure 3. Except during nesting, brood rearing, and moulting, F24 and M08 were found within 10 m of one another between 80 and 100% of the times they were located. Separation between the two peaked during incubation and again when the male began the wing moult, but except when the female was incubating, the two always came together to roost at night.

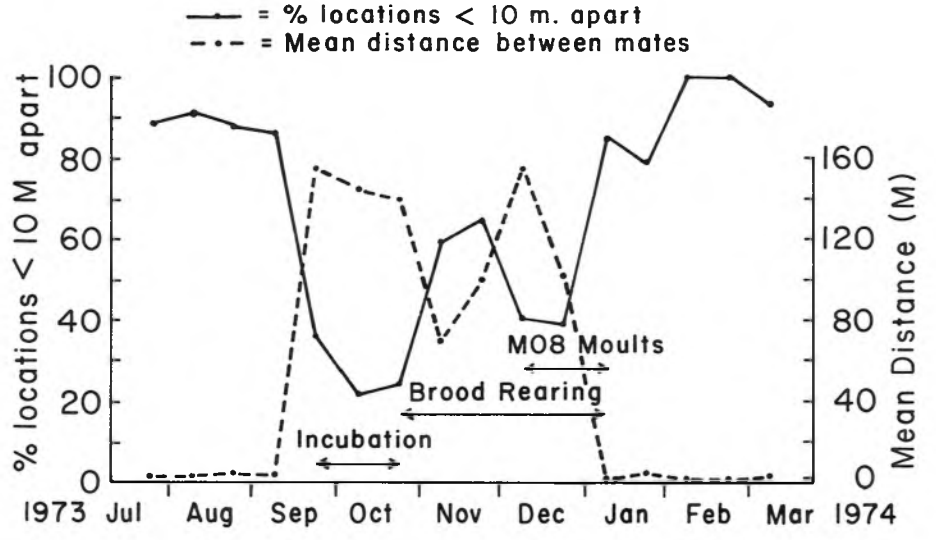

Figure 3. Spatial relationships between M08 and F24 from July 1973 to March 1974. A total of 1,158 locations is summarized.

We have seen no evidence that male Black Ducks accompany females with broods except at night and occasionally during territorial conflicts with neighbouring pairs. From conclusion of the wing moult until beginning of nesting the following year, the few separations of mates which were detected usually occurred when one or both members of a pair became involved in a territorial chase and the two did not reunite immediately afterwards. A second situation which occasionally led to separation of mates was when one pair member awoke before its mate and began to feed. Few if any separations of mates were caused by predators or humans flushing the birds: firm pairs made effective use of pre-flight intention movements (McKinney *et al.* in press). Their takeoff and flight was noticeably more synchronised than in pairs with new or tentative bonds.

Though rapid and complex changes of mates can occur when Black Duck pair bonds are being formed (McKinney *et al.* in press), the bonds of territorial pairs often lasted a year or more once they were established (Figure 4). F06/M04 were known to have been paired for at least 34 months (though a short break in the bond and a weakening of the bond during a liaison were

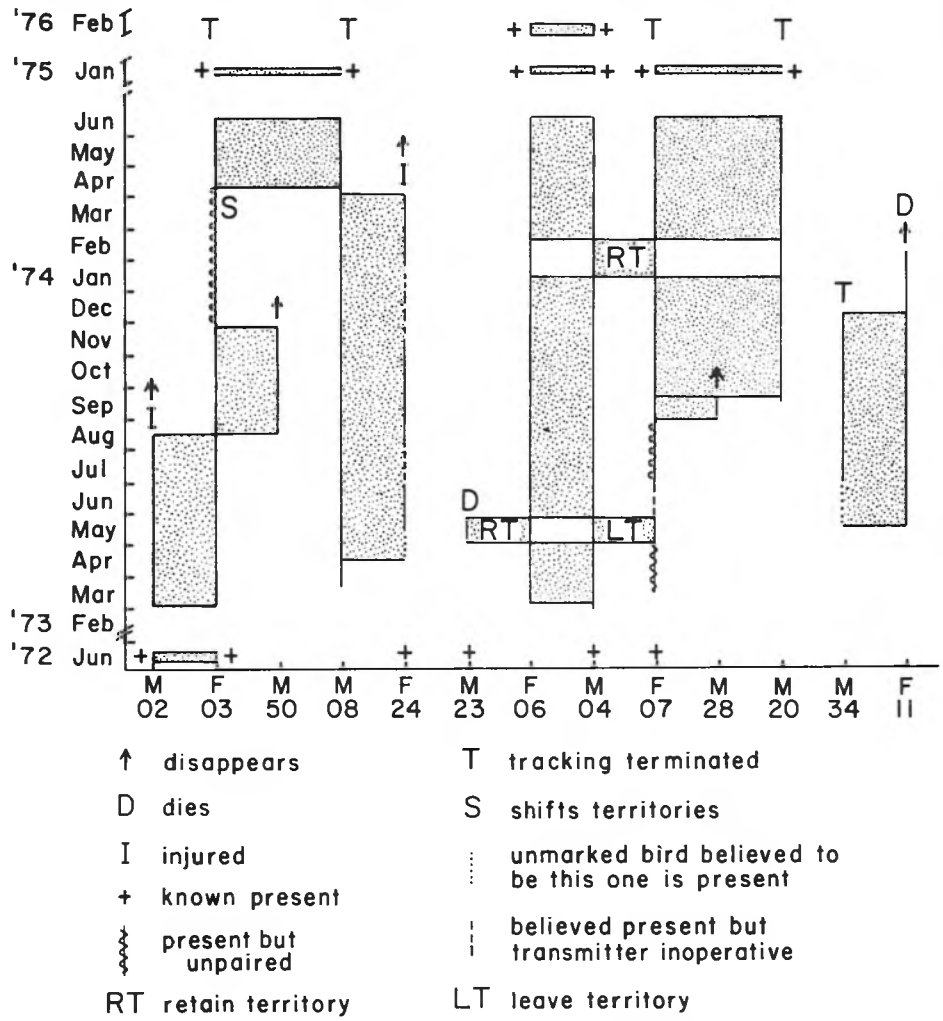

Figure 4. Long term history of pair bonds and liaisons between territorial Black Ducks on the Eerste River. Shading represents a pair bond or liaison between the individuals indicated. A temporarily bigamous relationship existed between F03, M50, and F07 during August 1973 (see McKinney *et al.* in press).

documented). Minimum durations of other well-documented long term bonds are: 21 months (F07/M20), 14 months (F03/M08), and 11½ months (F24/M08).

Of the 13 territorial Black Ducks we studied intensively along the Eerste, five were females and eight were males. Five types of take-over of mates or territories were recorded (Figure 4):

1. A male (M50, M23, M04, M28, M20) replaces the resident territorial male, gaining a territory and a mate. This usually involves defeating the resident male in one or more fights.
2. A female (F07) infiltrates an area, attracts mate(s) (M50, M28, M20) and the pair displaces former residents.
3. Birds of opposite sex (F07, M04) form a temporary liaison and retain residence while their respective mates (M20, F06) are in moult.
4. A male (M04) forms a temporary liaison with an unpaired female (F07), having lost his mate (F06) and territory to another male (M23).
5. After the disappearance of a female (F24), the resident male (M08) succeeds in holding the territory and attracting a new mate (F03). F03 was the only bird known to stay on the river but shift territory location.

While we have no record of an unmated female defeating a resident territorial female and replacing her in pair bond and on territory, this may be due to small sample size rather than to any real difference between the sexes in this respect.

Pair bonds in the territorial Black Ducks studied along the Eerste were most often terminated by disappearance or death of one member of the pair (Figure 4, Table 1). Of the six bonds terminated by loss of a mate, three were known to involve injury or death (M23, M02, F11). A fourth disappearance (F24) may also have been injury-related but nearly two months passed between detection of the injury and her disappearance, so we cannot say whether the two events were related. All documented deaths or disappearances except two (M50, M24) occurred during known periods of social strife, and we believe that fighting is a major cause of displacement and death of territorial birds.

Use of dams by territorial pairs

Black Duck pairs holding territories on the Eerste also made occasional use of the dams adjacent to the river. Of 7,995 locations recorded for these birds, 142 (1·8%) were on dams. We were unable to detect a seasonal pattern of dam use by Eerste River territory owners, though such a pattern might be

Table 1. Circumstances surrounding deaths or departures of territorial Black Ducks on the Eerste River.

Bird	Date	Occurrence	Remarks
M23	26 May 1973	Dies	Cause of death unknown—carcass eaten by predator/scavenger. Replaced M04 on territory and as F06's mate on 1st May 1973 but is replaced by M04 about 26th May 1973.
M02	16 Aug. 1973	Disappears injured	Bird can barely fly due to unknown disability. Has had conflicts with, and is replaced by, M50 on territory and as F03's mate.
M28	16 Sept. 1973	Disappears	Is defeated in conflicts by M20. Is replaced by M20 on territory and as F07's mate.
M50	26 Nov. 1973	Disappears	
F11	6 Feb. 1974	Disappears—Dies	Severe battle with F24 on 30th January 1974. Found dead of unknown causes 18th February 1974. Band returned but carcass not examined.
F24	1 April 1974	Disappears	Severe battle with F11 on 30th January 1974. Neck injured in area where fighting Black Ducks grip opponents. Injury detected 1st Feburary 1974.

expected if use of dams was caused by low water levels in the river. Seventy-two percent (102 of 145) of all locations at dams were recorded at night. Persistent disturbance of the birds during trapping efforts forced some birds to use dams, as did severe pressure from conspecifics. An example of the latter occurred during March of 1974. Previously, F03 and her mate had been found on dams only 11 times in 1,547 locations (0·7%). Having lost her mate, she was under intense pressure from pair F07/M20, and she was on a dam during 12 of 43 (28%) locations recorded during March. After moving to a new territory and pairing with a new male, F03 was not found on a dam once during the next 3 months (33 locations). It is not totally clear whether birds with river territories attempted to defend the dams during the infrequent visits, but we suspect that they did not.

We know of only two instances where Black Duck pairs took up territories centred on dams, rather than on rivers. One of these pairs (F43/M13, see Figure 10) also used two irrigation ditches which ran through the territory. The ditches were well-vegetated and could almost be considered as very narrow rivers. Approximately 40% of the locations of this pair were on the ditches and the female nested (unsuccessfully) within 1 m of a ditch. Pair F43/M13 disappeared in November 1973. The only pair known to have attempted to defend a territory with no flowing water was on Groote Zalze Dam (see Figure 10). This pair bred successfully on the dam in 1973, but took up permanent residence on the adjacent Blaauwklip River in August 1974. That neither of the two dam territories were claimed by other pairs after their original owners left supports the idea that Black Ducks strongly prefer river habitats (Siegfried 1968; Siegfried *et al.* 1975).

Patterns of activity, movement and habitat use

Black Duck activity as determined from radio signal fluctuations, showed a clear diurnal pattern with the major peak near sunrise and slightly less pronounced peak near sunset (Figure 5A). Over 80% of the morning (0400–0959 hours) signals were recorded as active, while in the evening (1600–2059) slightly over 70% were active. In contrast, during night time (2100–0359) and midday (1000–1559) only 19% and 35% respectively of the signals registered as active. Black Ducks typically repeat a feed-bathe-preen-sleep behaviour sequence throughout the daylight hours (McKinney *et al.* in press), and it appears from the radio telemetry activity data that the resting spells

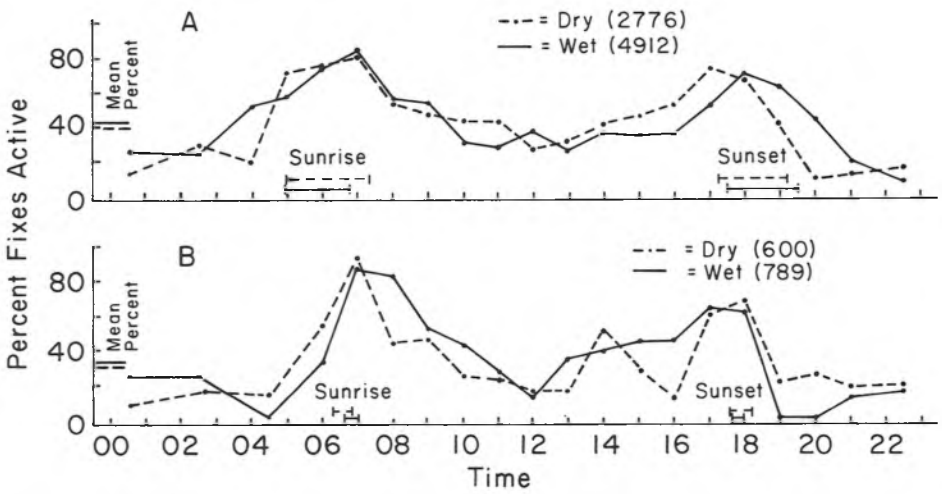

Figure 5. Signal activity patterns of radio-marked Black Ducks on the Eerste River. In A, 'Dry' represents December through April and 'Wet' represents May through November; each data point shows the proportion of 45 or more locations which were recorded as active. In B, 'dry' represents April and 'wet' represents August; minimum sample size is 12 locations. In both A and B, numbers in parentheses show total locations summarized, and data points plotted at midpoints between hours indicate that data for the 2 hours were pooled to reach the minimum sample size. Note that the figures on mean percent active are 'weighted' to account for the fact that relatively more locations were recorded during daylight hours when activity rates were relatively high.

must be relatively longer during midday. Mean percent activity was about 40% and, like the diurnal pattern of activity, varied little between wet and dry seasons. Considering the magnitude of changes in water levels and related feeding conditions, this similarity is somewhat surprising.

The daily activity peaks shown in Figure 5A are misleadingly low and broad, since data from several months are pooled and sunrise-sunset spans are broad. Figure 5B more closely reflects the true shape of peaks and their relationship to sunrise and sunset. Again, pattern and overall activity rates are similar, even though in April river levels were at their lowest, while in August river levels were uniformly high.

Since data from many birds are pooled in Figure 5, however, seasonal changes in activity rates may be masked. That such changes do occur is indicated by activity records for F24, who was recorded as active for 83% of all locations recorded within 45 days after her brood hatched (Figure 6). Her activity rate declined significantly from mid-brood to late brood phase and declined again to the post-brood phase. Sample sizes were inadequate for an hour-by-hour analysis, but night-time activity rate was extremely low (7%) during the brood period. Daytime activity rates were higher than for any other bird (92% during early and mid-brood phases).

The activity rate of F06 declined significantly during the wing moult (Figure 6) and this pattern was typical of moulting birds. Most moulting occurred when river levels were low, and flightless birds seemed reluctant to cross sections of dry or nearly dry stream bed between pools. Since most pools on the Eerste River are less than 100 m in length, moulting was associated with a substantial reduction in mobility. Even within a pool, moulting birds moved around relatively little and were difficult to observe even when they stayed close to one of our blinds.

No objective tests were done to determine which types of behaviour produced active signals, but by listening to signals while watching the marked birds, we gained a general impression of this relationship. Most feeding (we estimate 90–95%) produced an active signal. The only feeding behaviour which did not produce an active signal occurred when ducks remained almost stationary while straining mud in shallow water. Other activities which usually produced active signals included swimming, bathing and social interaction. Sleeping, resting and most preening were accompanied by inactive signals. While we do not know what proportion of active signals can be ascribed to feeding, we are confident that active signals produced by bathing, swimming and social interaction were far more common than were inactive signals during feeding. Thus Figure 5A suggests that, on a 24-hour basis, the Black Ducks we tracked fed less (perhaps considerably less) than 40% of the time.

A second measure of bird activity may be extracted from the radio tracking data—the tendency of birds to change locations (Figure 7). When compared to activity deduced from signal fluctuations, activity indicated by movements was relatively lower at dawn but high and more variable later in the morning.

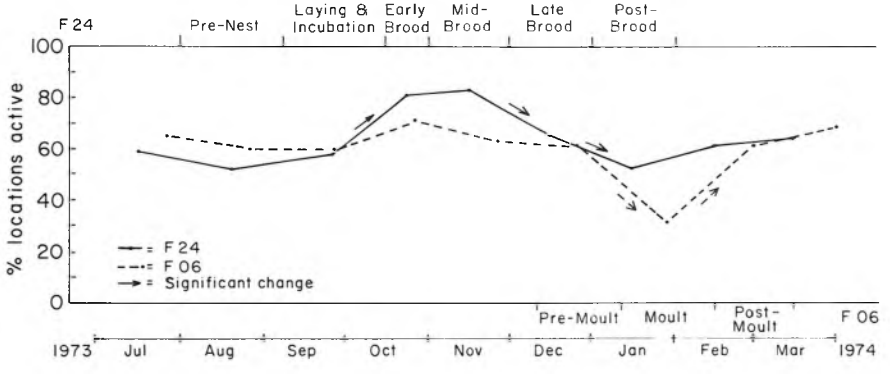

Figure 6. Percentages of radio signals classified as active for two female Black Ducks. Arrows represent significant differences between subsequent data sets for each bird (χ^2 tests, $p < 0{\cdot}05$). Because most locations were recorded when the birds were likely to be active, these data cannot be taken to reflect mean percent active on a 24-hour basis.

In the evening, movement activity showed two clear peaks versus one for signal activity. The two-peak pattern occurred as birds moved to a feeding area before sunset, fed intensively but in a small area, and then usually moved off to a favourite roosting spot for the night.

Night roosts were the most predictable spots used by the Black Ducks we tracked, but even these were sometimes shifted in response to disturbance or to encroachment by neighbouring pairs. For example, pair F06/M04 atypically roosted at the downstream end of their territory after a day of overlap and conflict with their neighbours (Figure 8).

Individual pairs altered their patterns of use of their territories with changing

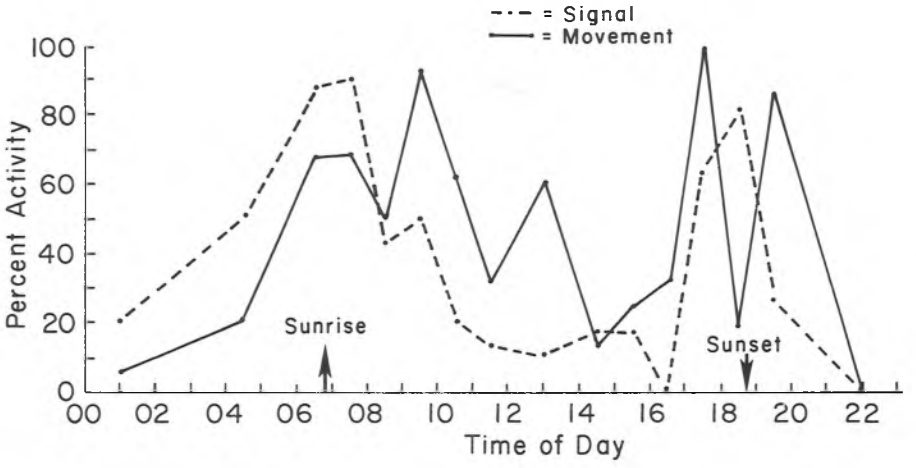

Figure 7. Signal activity (dotted line) and movement activity (solid line) in relation to time of day for two Black Duck pairs. Movement activity was considered to have occurred when two consecutive locations about 1 hour apart showed that a bird had moved more than 20 metres. Number of usable consecutive location sets = 259. The locations were recorded during three intensive tracking sessions during late March and early April 1973. Data from 0000–0259, 0300–0559, and 2000–2359 were pooled to reach minimum sample size of 10.

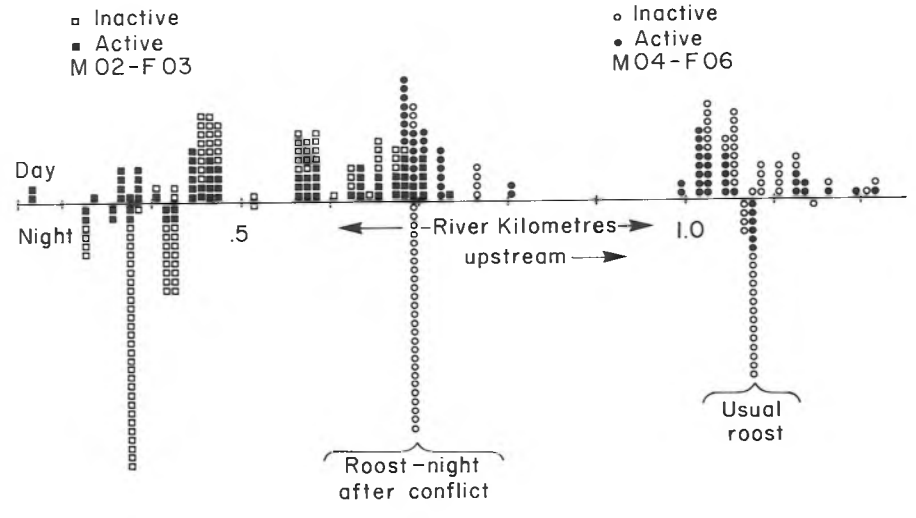

Figure 8. Activity patterns and distribution of locations of two Black Duck pairs during day and night. Day is defined as the period from one hour before sunrise until one hour after sunset. The locations (N = 322) were taken during three intensive tracking sessions during late March and early April 1973.

ecological conditions, particularly water levels. The gap between territories which existed at km 1·5 during the dry season (see Figure 2) was apparently due to the unsuitability of that stretch when water levels were low. This segment of the river lacked pools and averaged only about 1 m in width. The narrow channel was flanked by tall grass, which offered excellent feeding conditions when flooded during the winter, but little feeding opportunity and probably increased risks of predation when dry.

During the wet season, locations were well distributed over the territories, but the deeper, more permanent pools were more heavily used during the dry season (Figure 9). Even at the peak of the dry season, Black Ducks used most of the river within their territories at least sporadically, and we often saw them foraging on dry rocky river bed 10 m or more from water deep enough for swimming. Figure 9 summarizes information from only one pair, and patterns of habitat use were perhaps the most variable aspect of Black Duck spatial behaviour we studied. The discrete nature of pools depicted is partly a function of our arbitrary classification of pools as deeper than 20 cm. In reality, a Black Duck territory on the Eerste River is a mosaic of almost continually shifting patterns of water depth, shoreline substrate, and water velocity, all of which must influence use patterns. In addition, of course, social factors further complicate the pattern of river use by territorial pairs.

Non-territorial birds

In addition to the territorial pairs which have been considered up to this point, we radio marked and attempted to track other Black Ducks whose behaviour was very different. Figure 10 contrasts the movement patterns of several of these birds with movements of territorial birds. Pair F10/M09 were initially trapped on the Eerste River and were tracked and observed intermittently for 14 months. The most obvious difference between this pair and territorial pairs was that they moved over a much larger area (more than 850 ha versus 29 ha for pair F43/M13). Even the 29 ha territory of

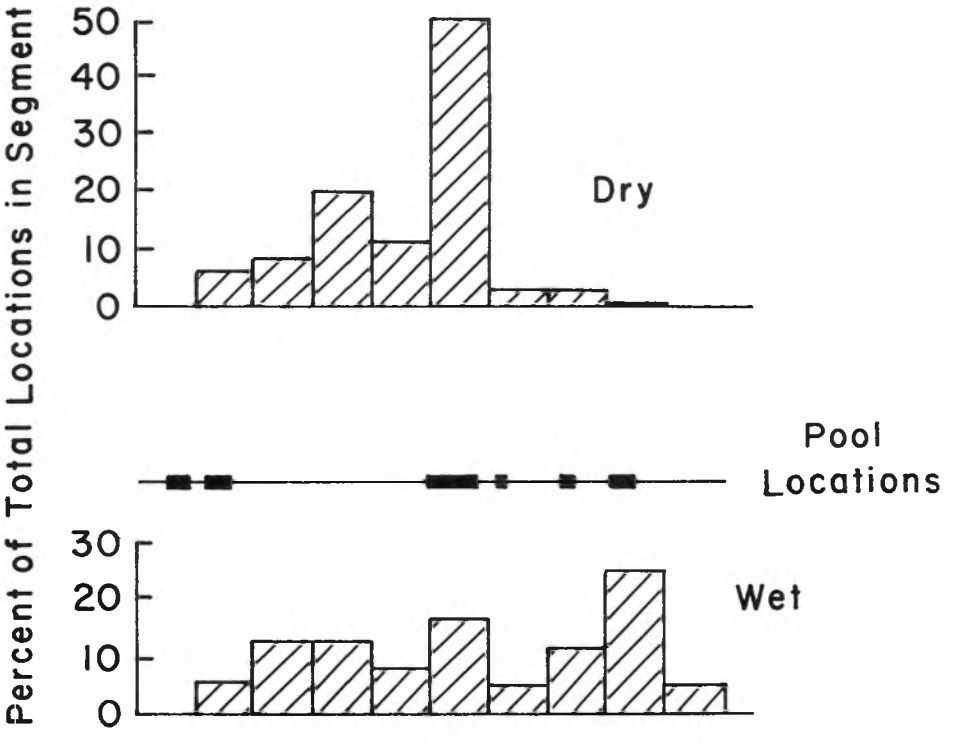

Figure 9. Distribution of locations of pair F06/M04 in relation to pools during dry and wet periods. Pool = river segment at least 20 cm deep at low water level.

F43/M13 is atypically large compared to river territories because of the spatial arrangement of the dams and subsequent inclusion of considerable unused upland area. In the more typical situation of a river territory, size would be approximately 0·67 ha (670 m long by 10 m wide). F10/M09 were located only 114 times over 14 months, as against 500 to 2,000 locations of the territorial pairs. They occasionally disappeared from the usual haunts and could not be located for up to three months. We saw them leaving for, and returning from, areas to the northwest of their usual range, but could never locate them there on the ground. In contrast to territorial pairs,

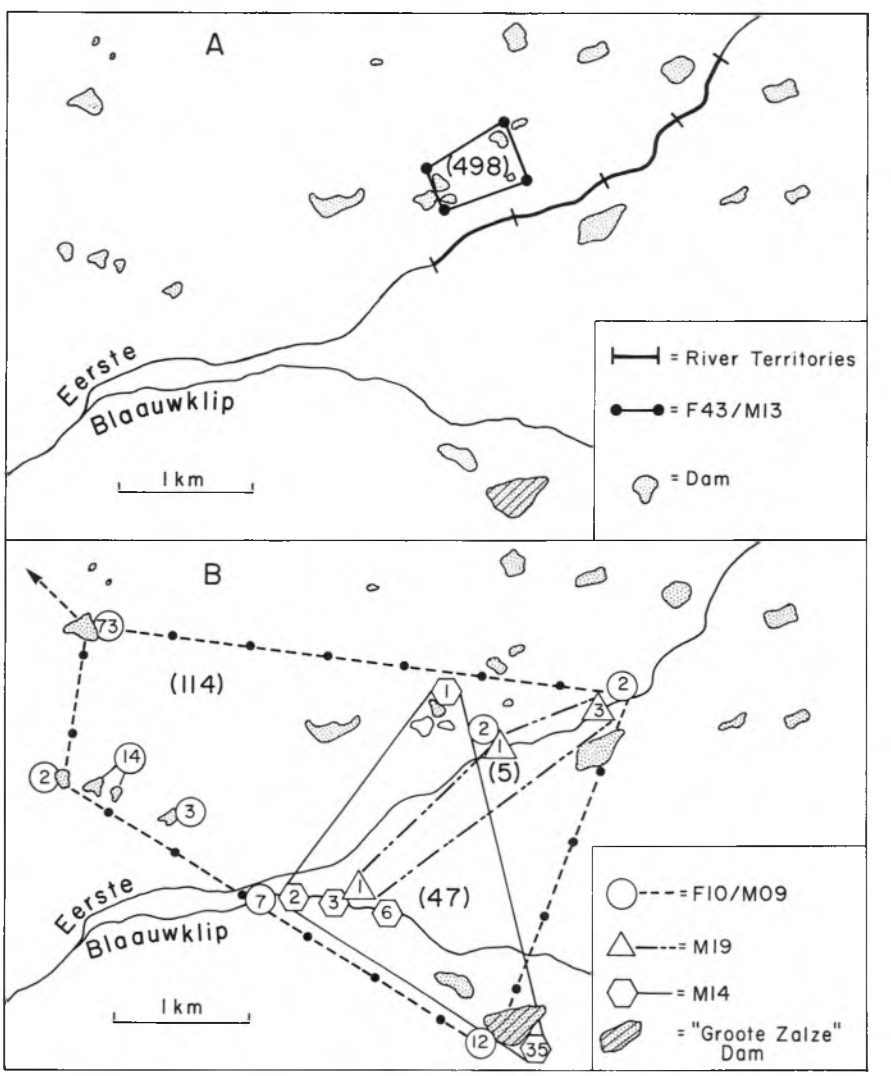

Figure 10. Comparison of the movement patterns of territorial (A) and non-territorial (B) Black Ducks in the Eerste River Valley. In A, the numbers in parentheses are the total locations recorded for the pair. Approximately 8,000 locations of the residents on the river territories were recorded. In B, numbers in parentheses are the total locations recorded, and numbers in symbols show the numbers of locations recorded in general areas. Territorial birds could usually be located at any time, but non-territorial birds were often difficult to find. Hence, non-territorial birds were located only sporadically and the indicated contrast in area used should be considered a minimum.

F10/M09 avoided many water areas within their home range. They were located most often on dams, but were found twice on the Eerste River and sporadically on a 200 m stretch of the Blaauwklip—a narrow, shallow stretch not know to be used by a territorial pair. They were never seen pursuing other Black Ducks as territorial birds did, and seemed to avoid areas where encounters with territorial birds were likely.

The relatively stable pair bond of F10/M09 was exceptional among non-territorial birds: all of the others were either unpaired or were seen with several partners. F10/M09 were usually seen together, but each was seen alone on several occasions. Given the inadequate tracking record on these birds, it is possible that they too maintained association or liaisons with other birds. None of the non-territorial birds were known to breed and most frequented Groote Zalze Dam where they interacted socially with other Black Ducks and roosted (see Siegfried *et al.* 1977; McKinney *et al.* in press). In addition to using dams and marginal river habitats, non-territorial birds sometimes used places within other birds' territories where they were relatively unlikely to be discovered by the territory owners. Such locations included pools away from the main channel, places where irrigation ditches converged with the river, undercut banks, and tangles of dense brush.

Out of 30 adult Black Ducks trapped on the central 3·4 km of the Eerste River, 16 (53%) were known to be sedentary and territorial for a month or more. Of 136 Black Ducks seen during two censuses of waterfowl over 67 km^2 in the Eerste River Valley, Siegfried *et al.* (1975) noted that 78 (57%) were paired and on rivers. Both percentages have major limitations as estimates of the actual ratio of territorial to non-territorial birds in the population, but do serve to demonstrate that a substantial proportion of the population was not holding territory and thus was not breeding. At the beginning of the breeding season, this segment of the population was known to include males and females of both juveniles (fledged the previous season) and older birds.

Territory size and non-territorial birds on the Klipplaat River

The territorial pair tracked on the Klipplaat River ranged over 1,458 m of river during the ten days we studied them. Only two instances of use of this area by other birds was seen; one of these resulted in immediate expulsion by the territorial pair, and the other intrusion was not immediately detected by the residents. We were able to locate these birds each time we attempted to do so, and this pair seemed generally comparable in movement patterns to the territorial pairs on the Eerste, except that territory size was roughly double that on the Eerste.

In contrast, the other two birds successfully tracked on the Klipplaat did not appear to be territorial. They were never seen in territorial chases and we often could not find them on the four kilometres of river searched daily. Two censuses of 11·3 km of river were centred on the area where these two birds were marked, but failed to account for them. We presume they must have been on more distant portions of the river or on one of the few stock dams in the area. Thus, though sample sizes were small and tracking duration short, records from the Klipplaat river suggest that non-territorial 'floaters' exist in areas where territories are relatively large, as well as in crowded populations such as on the Eerste.

Pair densities in relation to characteristics of rivers

Density of African Black Duck pairs in relation to some physical and biological characteristics of different rivers is summarized in Table 2. On rivers where pair density was low in relation to the length of segment studied (i.e. the Klein Berg, Natal Rivers and Mooi), it is important to recognize that missing even one pair would have considerable impact on pair density figures. Data from the six Natal Rivers and the Mooi were provided by respondents to our questionnaire. Census techniques thus differed from ours, but the data are still useful in establishing the general range of pair densities to be expected.

Pair densities along the Eerste and Blaauwklip Rivers were nearly twice that of the next most dense population found elsewhere, and approximately nine times that of the lowest reported density (Table 2). Many factors could influence this variation, including physical and biological characteristics of the rivers.

We initially thought that the distance at which Black Ducks could see their neighbours might be an important determinant of spacing patterns (see Watson 1964; Watson & Miller 1971). Consequently we compared visibility indices for the Eerste, Blaauwklip, Klein Berg and Klipplaat Rivers. The visibility index on the Eerste was

Table 2. Density of Black Duck pairs on different rivers in South Africa.

River location	Metres of river per pair[1]	Kilometres of river studied	Method of study[2]	Visibility Index	Mean width[3]	Mean depth
Eerste (33°58′S 18°50′W)	670 m	3·4	RT-5	59·1 m	10 m	0·25 m
Eerste	657 m	8·1	C-2	—	12 m	0·40 m
Blaauwklip	785 m	5·4	C-2	50·2 m	3 m	0·15 m
Klein Berg (33°18′S 19°08′W)	2,514 m	5·0	C-2	60·5 m	9 m	0·40 m
Klipplaat (32°24′S 26°54′W)	1,458 m	1·5	RT-1	64·6 m	14 m	>1·0 m
Klipplaat	1,357 m	11·3	C-2	—	14 m	>1·0 m
Six Natal Rivers (≈30°S, 39°W)	2,500–6,000 m	5–12	C-2 to 3[+]	—	mainly 10–20 m	0·2–0·5 m
Mooi (29°22′ S 29°44′W)	4,000 m	4·2	C-3[+]	—	15 m	1·0 m

1. Equals territory size only if amount of overlap is assumed to be cancelled by vacant space betw territories and by chance of counting non-territorial pair on river. These constraints were roughly met or Eerste, but may not have been elsewhere.
2. RT = radio tracking, number = number of pairs tracked. C = census, number = number of replicates.
3. In this and following two columns, subjective estimates are underlined, estimates based on measurem are not.

not significantly different (t-tests, $P > 0{\cdot}10$) from either the Klipplaat or the Klein Berg, where territories were two to three times as large. The visibility index on the Eerste was significantly greater ($P > 0{\cdot}05$) than on the Blaauwklip but pair density on the Eerste was higher than on the Blaauwklip, contrary to the relationship expected if visibility were the major determinant of spacing patterns. Neither width nor depth showed a clearcut influence on pair density. The Blaauwklip was the narrowest and shallowest river considered, yet it supported nearly as many pairs as the much wider Eerste, and far more

Percent woody overstorey	Abundance & type of nearby static water[4]	Oaks += Present −= Absent	River description and comments	Data source
86	+++ irrigation dams	+	River has approx. 30% deep pools, remainder is rapids and riffles. Substrate (in order of frequency of occurence) is: cobble-boulder, sand-silt, bedrock. Pools may be isolated during dry season.	This study
90	+++ irrigation dams	+	As above. Lower stretches contain more deep, wide pools, fewer riffles and rapids.	Siegfried *et al.* 1975
95	+++ irrigation dams	+	Mainly quiet pools with few riffles or rapids. Substrate mainly sand/silt. Drying is more severe than on Eerste.	Siegfried *et al.* 1975
10	++ irrigation dams	−	River configuration, size, and substrate very similar to Eerste. Less subject to drying than Eerste.	This study
<05	+stock dams	−	River mainly deep pools with few rapids. Substrate bedrock and sand/silt. Less subject to drying than Eerste.	This study
<05	+stock dams	−	As above.	This study
?	?	−	Rivers vary from mainly rapids with few pools to slow-flowing with few rapids. Rivers are: Umlaas Buffels, Unsumdusi, Umgeni, Ngwagwane, Umgumkulu. All are less subject to drying than the Eerste.	R. R. K. Maguire (pers. comm.)
<10	+++ oxbows	−	River mainly quiet pools with few rapids. Oxbows and marshy areas adjacent to river along half its length. Less subject to drying than Eerste.	D. T. Row-Rowe (pers. comm.)

4. +++ = very common, ++ = common, + = rare.

than the other streams studied.

Presence of woody overstorey was higher on the Eerste and Blaauwklip (84%+, Table 2) than on any of the other streams studied. Indeed, this is one of the most striking associations shown. However, several of the other streams had considerable cover and shade suitable for Black Ducks, provided by herbaceous plants, brush piles, and bank undercuts.

The many irrigation dams in the Eerste River Valley could influence spacing of pairs on rivers in at least two different ways. Firstly, territorial pairs might require smaller territories if part of their needs were met by using dams. We discount this possibility because most territorial pairs on rivers used dams only occasionally, and then mainly as a refuge from disturbance. Secondly, the presence of many dams could support relatively higher populations of non-territorial birds than would survive if no

dams were present. Attempts by these extra birds to gain territories could then force territorial pairs to restrict the size of their territory in order to maintain full control of a stretch of river.

We know that territorial pairs may spend almost all their time over several days or more attempting to discourage intruders in one area and thus neglect defense of another part of the territory. The question remains as to how much effect 'pressure' from intruders may have on the small territory size in the Eerste River Valley, and to what extent the many irrigation dams influenced the number of non-territorial birds present. It should be noted that the Klipplaat River supported higher pair densities than the Klein Berg, even though dams are less abundant along the Klipplaat (Table 2).

Perhaps the most meaningful comparison of rivers listed in Table 2 is between the Klein Berg and the Eerste. These two rivers were only 80 km apart and very similar in depth, width, substrates and general configuration. Trees were smaller along the Klein Berg, producing less woody overstorey than present on the Eerste, but palmiet *Prionium palmita* produced substantial amounts of shade and cover, as did brush piles and undercut banks. Irrigation dams were less common along the Klein Berg than in the Eerste River Valley, but were fairly common nonetheless and Black Ducks were seen on them. In spite of these similarities, the Klein Berg supported just over a quarter the density of Black Duck pairs as does the Eerste. Conversely, habitat conditions on the Klipplaat were very dissimilar to those on the Eerste, yet the Klipplaat supported roughly half the density seen on the Eerste.

The presence of oaks had considerable impact on the feeding ecology of Black Ducks on the Eerste and Blaauwklip rivers, and may have influenced spacing patterns as well. Oak trees were introduced into the Eerste River Valley in the late 1600's and are now well distributed along both the Eerste and the Blaauwklip. Oaks formed part of the overstorey in 53 (28%) of 213 sampling points along the Eerste. We observed Black Ducks regularly eating acorns. Feeding birds appeared actively to search out fallen acorns in the riverbed and even resting birds would become alert and move to eat new-fallen acorns. Furthermore, acorns could commonly be felt in oesophagi of captured birds. Thus Black Ducks in the Eerste River Valley where territories were small had access to, and made considerable use of, a substantial food resource which was unavailable on the other rivers where territories were large and populations were low.

Discussion

The spacing and pairing system

The territorial system of the Black Duck is perhaps the most spatially discrete arrangement yet documented in any species of waterfowl. Except during takeovers of mates and/or territories, overlap between adjacent territories is minimal. At least on the Eerste River, residence, pair bonds and territories are commonly maintained year-round. Such stable and discrete systems are rare in the subfamily Anatinae, but may also exist in other river specialists including the Torrent Duck (Johnsgard 1966), the Blue Duck (Kear & Steele 1972) and Salvadori's Duck (Kear 1975). It is thus appropriate to carefully examine those characteristics of Black Duck habitat which we believe have tended to promote stable residence and pair bonds, as well as strict territoriality.

On a seasonal or *short term* basis (i.e. through the year), the Black Duck rivers which we have studied appear to be more stable than the naturally ephemeral ponds and marshes often exploited by breeding ducks of many species. Black Ducks are thus able to maintain year-round residence at least over much of their range. Advantages accruing through permanent residence would include knowing the resources, competitors and predators present, and avoiding the energy costs and risks of moving to seasonally alternate habitat twice each year. The natural scarcity of alternate static-water habitats over much of southern Africa and the presence of species better adapted to using those waters must also have reinforced year-round residence where it was possible. Effective territorial defense in the Black Duck depends on close cooperation between mates, which would favour long-term pair bonds (McKinney *et al.* in press). Once a pattern of year-round residence and territoriality existed, any pairs attempting only seasonal residence would have faced poor odds indeed in attempting to establish territories on which to breed.

The relative stability of rivers on a long-term basis (i.e. year to year) may also have been important in development of the spacing system seen in Black Ducks. The capacity of rivers to support breeding birds may change somewhat from year to year in response to changes in water levels (though we have no direct evidence of this from the

Eerste). Nonetheless, the amount of such changes must be minor when compared to the vast fluctuations in more ephemeral types of wetlands. If rivers are indeed relatively stable from year to year, Black Duck populations would also be expected to remain relatively stable, and probably closer on average to carrying capacity than would species exploiting unstable habitats. Thus competition would be more intense, or at least competitive ability would be selected for more consistently.

Brown (1964) envisaged that competition for a critical resource that is economically defendable (considering the time, energy and risks involved) favours the development of territorial systems. Specific resources within Black Duck territories support virtually all of the activities of the pair including daily matters such as feeding and bathing, as well as essential seasonal activities like nesting, brood rearing and moulting. It is difficult to determine the relative importance of each.

Limited or low food resources in rivers have been suggested as a factor promoting solitary existence or territoriality in river specialising Anatids (Johnsgard 1966; Siegfried 1968; Kear & Burton 1971). Documentation of the distribution and relative abundance of food in rivers versus static waters is very difficult, and the issue is confused on the Eerste and Blaauklip by the relatively recent addition of the substantial acorn food resource. While we know that acorns were used virtually year-round in the Eerste River Valley, we know almost nothing about the other types of food consumed or their patterns of distribution and availability.

Black Ducks may invest considerable amounts of time and energy in aggressive encounters when the situation requires it (McKinney *et al.* in press), and we believe that these encounters involve substantial risk of injury to the birds involved. It must be remembered, however, that the costs of *not* having complete control of a territory are great indeed; in most cases, losing (or failing to gain) a territory means that chances for reproduction are nil. A major portion of the population (perhaps about 40 to 50%) fail to obtain a territory and consequently fail to breed.

The evolution of strategies of investment (time, energy, risks) by Black Ducks in initially establishing territories may have been influenced by the relatively long period of potential gain once the territory is established. Though territories require continual investment to maintain, the initial cost may only need be met once over perhaps two or more years.

The time and energy required for residents to detect trespass is much less on a river than on the breeding habitat used by many species. Since the water body involved is relatively narrow, swimming or even flying along it makes detection of trespassers likely unless they are completely hidden. Hiding places do exist along the Eerste River and probably along most rivers inhabited by Black Ducks, but the dense stands of emergent vegetation common to many static waters are rare. Furthermore, the energy costs of downstream travel in a river can be minimized by utilizing the current. In upstream travel, the current is largely avoided by swimming in slack water along the edge or by flying.

We have argued that the relative stability and the open, contiguous nature of river habitats may have been among the factors promoting the evolution of a territorial system in the Black Duck. These two habitat characteristics would also seem to be present along the shorelines of large, deep, permanent bodies of water as described by Weller (1972, 1976) for Crested Ducks *Lophonetta specularoides* and Steamer Ducks *Tachyeres* spp. It thus may eventually be enlightening to compare the spacing patterns of 'shoreline' duck species to the patterns seen in closely related species which use habitats that are more 'closed' and less stable and contiguous. Such a comparison would also have to take spatial and temporal distribution of food into account.

Territory size

Territory size is small and populations are high (perhaps abnormally high) in the Eerste River Valley. We envision two major possible explanations for this fact, while recognizing that the two are not mutually exclusive and that several sub-mechanisms could influence each explanation. The first possibility is that *territories are small because of pressure from neighbours and non-territorial birds.* At least in a short-term sense, pressure from intruders can indeed force territorial pairs to neglect the defense of other parts of their territory. It is also clear that, during parts of the year at least, any undefended stretch of the river is soon discovered by prospecting non-territorial birds or by neighbouring pairs. The record of F07 (Figures 2 and 4) reinforces the point that *any* use of a territory by an intruder, even if that use is at first sporadic and inconspicuous, can pose a serious threat to the

continued territory ownership by the resident pair. It thus appears that persistent intrusions could force territorial pairs to consolidate their efforts in order to maintain complete control (which they apparently must do at all costs). Faced with relatively high populations of prospecting non-territorial birds, territorial pairs may simply have no option other than to defend a smaller area more intensively. To test this possibility adequately, one would need to monitor the rate and intensity at which encounters occur in dense versus sparse populations. Our work on the Klipplaat River shows that non-territorial birds were present, albiet probably in lower numbers than in the Eerste River Valley. Subjectively, aggressive encounters seemed quite common on the Klipplaat (four were seen in ten days). However, the frequency of chases varies seasonally and from day to day depending on the particular social interaction which happens to be occurring at the time (McKinney *et al.* in press). For this reason, ten days is too short a span from which to draw a firm conclusion as to the overall rate of interactions.

High populations of non-territorial birds which maintain themselves in the Eerste River Valley by using dams primarily and rivers furtively would be forced to emigrate if the dams were not present. Without the alternative habitat provided by the dams, mortality would probably be quite high among displaced birds.

The second possibility is that *territories are small because the resource needs of the pair are met in a relatively short segment of river.* The Eerste and Blaauwklip could simply represent ideal Black Duck habitat in terms of distribution and interspersion of habitat components such as cover, nesting sites, moulting sites, or roosting sites. However, unless subtle differences which we have not yet recognized are very important, it is difficult to accept this interpretation, particularly in a comparison of the Eerste, Klein Berg, and Klipplaat rivers (see Table 2). Thus the presence of a very rich food supply seems to be the most intuitively acceptable resource variable under this option.

Positive correlations between richness of food supplies and population density are common (see Watson 1971) though interpretations of this relationship have been diverse. Even where actual impacts of nutrition on spacing behaviour have been documented, they have not necessarily been simple or direct (Watson & Moss 1972).

With the establishment of oaks in the Eerste River Valley approximately 250 years ago, Black Ducks were presumably subjected to a relatively abrupt and extreme change in the amount and type of food available. This supplementation of food resources could easily have meant that adults needed less habitat in which to feed. At present, territorial pairs exist on the Eerste River in densities perhaps twice that on most rivers and yet food supplies are apparently adequate. Ducklings, however, are faced with a relatively small area in which to feed, but are afforded no supplementation of diet. Due to their size, acorns are totally unavailable to ducklings, and would be poor fare for young ducklings anyway because of their low protein content. This problem is compounded on the Eerste by siltation, water diversion and other human influences which probably reduce the availability of invertebrate food stocks.

In a more natural river system, adults and ducklings probably utilize more similar food items so that a territory large enough to support the pair year round is also large enough to support the brood. That ducklings on the Eerste actually do face food supply problems is supported by several lines of evidence; (1) females and broods make persistent efforts to use parts of their neighbours' territories (Figure 3), (2) activity rates of females with broods are higher than rates of other birds (Figure 6), and (3) broodmates exhibit evidence of direct competition for food and some show signs of severe nutritional deficiency (unpublished data). For whatever reason or combination of reasons, it appears that territory size on the Eerste River is very close to the minimum size which is needed to support successful reproduction under present conditions.

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Summary

Territorial Black Duck pairs maintain remarkably tight control over their section of river. About 90% of the territory is effectively defended against use by neighbouring pairs, although non-territorial birds can sometimes hide and temporarily escape detection. Hens with broods trespass overtly although most brood rearing occurs on the parental territory. Spatial ties between mates are exceedingly close and pair bonds in territorial birds may last two or more years. Dams adjacent to the river are used only infrequently by pairs holding territories on the river. Few pairs set up territories on dams, though non-territorial birds often used dams. Non-territorial birds do not breed, and they make up a sizeable portion of the total Black Duck population. Non-territorial birds exist in both dense and sparse populations.

Characteristics of rivers which may have favoured the evolution of the spacing and pairing system seen in Black Ducks include short- and long-term stability, and the contiguous, open nature of the habitat which makes detection of trespass relatively efficient. Territorial Black Duck pairs in the Eerste River Valley are about twice as dense (territories are about half as large) as the densest population found elsewhere. This may be due to pressure from conspecifics, to abundant resources (particularly food) for the territorial birds, or to a combination of the two.

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Above: male African Black Duck *Anas sparsa*. (*Philippa Scott*)
Below: male Common Goldeneye *Bucephala clangula*. (*Joe B. Blossom*)