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BEHAVIORAL AND VOCAL AFFINITIES OF THE AFRICAN BLACK OYSTERCATCHER (*HAEMATOPUS MOQUINI*)

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The African Black Oystercatcher (*Haematopus moquini*) is endemic to southern Africa, occurring as a breeding species from the Hoanib River mouth in Namibia around the Cape of Good Hope to Mazeppa Bay, Transkei (Hockey 1983a, S. Braine, in litt.). *H. moquini* has wholly melanistic plumage and, like other Old World species, adults have scarlet irides, bright coral-pink legs and jet-black feathers on the back. Its systematic relationships are problematical, some authorities (e.g., Peters 1934; Larsen 1957) preferring to treat it as a subspecies of the European Oystercatcher (*H. ostralegus*), whereas others accord it full species status (e.g., Heppleston 1973; Clancey 1980).

Recent studies have revealed details of the general biology of *H. moquini* (Summers and Cooper 1977; Hockey and Cooper 1980; Hockey 1981a, b, 1982, 1983a, b, c, 1984; Hockey and Branch 1983, 1984; Hockey and Underhill 1984). Despite this wealth of ecological knowledge, the only report of the breeding behavior of this species is that of Hall (1959), which is based on relatively few birds and does not cover the repertoire of known behaviors of oystercatchers (see Makkink 1942, Williamson 1943, Miller and Baker 1980). Vocalizations of *H. moquini* have not been studied previously. In this paper we describe the behavior and vocalizations of African Black Oystercatchers during the breeding season in the southwestern Cape Province, South Africa. Our ultimate goal is to provide comparative data to assist in clarifying relationships within the Haematopodidae (Baker 1974, 1975, 1977).

METHODS

Observations of *H. moquini* were made principally during the breeding season early in 1982 (January 6–8, 13–15, and 20–24) at Marcus Island (33°02'S, 17°58'E) and Malgas Island (33°03'S, 17°55'E) in Saldanha Bay, southwestern Cape Province, South Africa. General observations on the behavior of birds on these sites in 1979 and 1980 were made by the second author. Motion pictures of displays were taken with an Elmo super 8 mm sound camera at 24 frames/sec to ensure good sound fidelity. Behavioral interactions among three territorial pairs were filmed from a portable canvas hide located within 20 m of the birds. Displays of birds with young were filmed at close range (ca 5–20 m) with the observers in full view. Figures of various displays were prepared by tracing images from still-frame projections. Descriptions of all display behaviors are based on terminology suggested by Cramp et al. (1983).

Tape recordings of all vocalizations were made at 19 cm/sec on a Uher 4200 Report Stereo IC tape recorder using Scotch 177 tape and a Dan Gibson parabolic reflector (model P-200) and microphone. Tapes were analyzed with a Unigon FFT Spectrum Analyzer and sonagrams and amplitude envelopes of vocalizations were prepared using a Kay Elemetrics Digital Sona-Graph 7800 set on a wide band filter (300 Hz) and the 80–8000 Hz range.

Whenever possible the sex of the displaying birds was recorded. At Marcus Island almost all birds had previously been color-banded with unique combinations of bands, and were sexed at the time of capture by the degree of distension of the cloaca. Females have visibly distended cloacas for up to 10 days after laying is completed (Hockey 1981b). Unbanded birds usually could be sexed by direct observation in "backlighting" views because the base of the bills of females is orange whereas in males it is reddish-orange, as has been noted for other species of oystercatchers (Miller and Baker 1980). Additionally, within pairs males of *H. moquini* commonly have a shorter and less pointed bill than their respective mates (Hockey 1981b).

BEHAVIOR

Copulation.—The only filmed sequence of copulation we obtained for *H. moquini* revealed specific posturing by both members of a pair. The female solicited copulation by assuming a stationary pre-copulatory posture in which she inclined her body forwards and pointed her head and bill downwards at about 45° to the ground. The male responded by approaching his mate from one side with the "stealthy walk" (Makkink 1942) in which his body was hunched noticeably, his head was drawn tightly into his breast, and the wings were raised slightly up and away from the body (Fig. 1A). Just before the male flew onto her back, the female crouched lower and raised and spread her folded wings outwards (Fig. 1B). The male balanced on the female by flapping his wings while sitting with his tarsi and feet along her back (Fig. 1C). Apparent cloacal contact was made by the male rotating his body backwards and downwards, and then arching his pelvic region forwards (Fig. 1D). The copulation was terminated soon after this when the female reached back and grasped the male's bill with her own, whereupon the male dismounted immediately (Fig. 1E–F).

On some occasions copulation was preceded by display behavior which closely resembled piping (see beyond). In this pre-copulatory display both birds of a pair walked forwards together with their bills held at an angle between 45° and 90° to the ground, after which copulation proceeded as described above. In the breeding season copulations were observed following the cessation of territorial disputes, aerial chases of intruding oystercatchers, and "butterfly flights." Copulations were also observed outside the breeding season from mid-winter (June and July) through early spring (near the end of August) when territorial interactions increased in frequency. Of 11 attempted copulations observed in winter and spring three

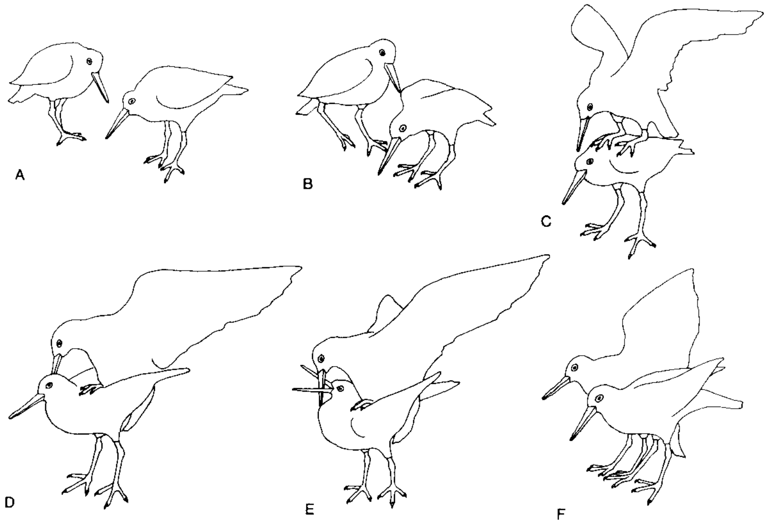

FIG. 1. Copulatory sequence (based on filmed sequence) by a pair of *H. moquini.* (See text for details).

did not culminate in cloacal contact, whereas all seven observed in the breeding season in January 1982 (when eggs were being laid on Marcus Island) were completed successfully. Copulations were brief, ranging in duration from 3–9 sec (mean duration ± SE = 5.9 ± 0.64 sec, N = 12).

Piping.—Piping displays on the ground were characterized by striking postures and vocalizations. A typical sequence of postures taken from one continuous piping display by a pair of birds when swooped on by a passing neighbor is shown in Fig. 2. In this example the male (Fig. 2A, right bird) began vocalizing while he held a posture in which the head was inclined downwards and forwards, the bill was almost vertical to the ground, and the wings were raised markedly at the carpal flexure and held away from the body. The female walked towards the male with the bill held vertically and began calling (Fig. 2B, left bird). She turned counterclockwise in this posture (Fig. 2C) and then performed a "parallel run" with her mate (Fig. 2D) covering a distance of approximately 15 m. Both birds halted at this point and turned to face each other, still continuing to vocalize loudly (Fig. 2E). Shortly thereafter the female stopped calling and stood upright (Fig. 2F), and then the male ceased calling too. Subsequently, he approached the female in a hunched pre-copulatory posture (Fig. 2G) and nudged her aside while performing "false-feeding" (Fig. 2H). Both birds concluded the display sequence by preening vigorously.

Piping displays were most frequent early in the breeding season when

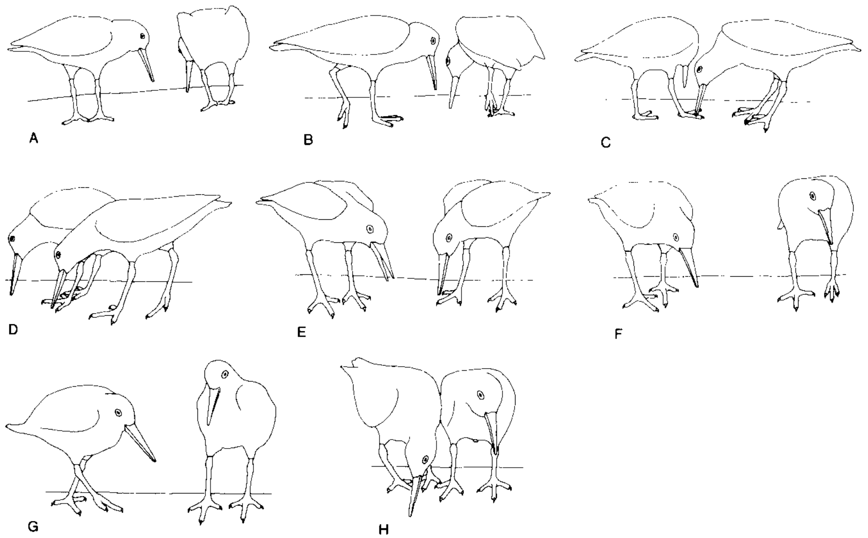

FIG. 2. Piping display sequence (based on filmed sequence) by a pair of *H. moquini.* (See text for details.)

birds were establishing and defending territorial boundaries. Intruders were usually repelled by mutual piping displays by both members of a pair, but when one bird was absent from the territory the remaining bird performed alone. As in other species of oystercatchers (see Miller and Baker 1980) piping displays in *H. moquini* were highly contagious, often attracting birds from nearby territories. The number of birds observed in piping groups varied from 2–17, but the usual number was three or four.

Groups piping on the ground sometimes wandered across several territories, but often they occurred in areas of suboptimal nesting and feeding habitat not occupied by territorial birds. Piping also occurred in flight when up to eight birds participated. Members of a pair piped in unison with their necks arched down and bills held vertically while flying in parallel formation, and this is clearly the aerial counterpart to parallel running on the ground. In both aerial and ground displays involving larger numbers of birds some of the participants adopted piping postures but remained silent. We never observed juveniles taking part in piping displays.

Distraction displays.—Breeding adults performed elaborate distraction displays in defence of young. One display, hereafter referred to as the distraction-lure display, has never been described for any species of oystercatchers (Fig. 3).

The high-intensiy form of the distraction-lure display was given re-

FIG. 3. Distraction-lure display of an adult *H. moquini*. Note the raised tail.

peatedly by parent birds (five of six displays were given by females) when we held their chicks in full view and especially when the chicks gave distress calls. All displays we filmed were very similar in that they were composed of sequences of exaggerated postures designed to attract attention to the displaying bird. In one such display the female responded to our presence by flying onto the top of a large rock within 5 m of our position, and then raised her folded wings asymmetrically away from the body while orienting directly towards us (Fig. 4A). At the same time she began calling rapidly. After holding this position for about 5 sec she then turned sideways on the same spot and began to slowly flap her wings (Fig. 4B). She gradually assumed a striking oblique posture by tilting her body forward so that the bill was at an angle of about 30° to the ground (Fig. 4C–E) and the tail was elevated slightly and alternately fanned and closed. About 22 sec later the female moved slowly away from us in a pronounced crouching posture while continuing to flap her wings (Fig. 4F). After jumping down from the rock to a wave-cut platform she broke into a slinking run (Fig. 4G) of about 20 m until she disappeared behind boulders. On several occasions the running bird crouched very low, arched its back, and depressed its tail (Fig. 4H) in a characteristic "crouch-run" (Cramp et al. 1983) before "hiding" in a crouched posture with the head and bill flattened along an exposed rocky crevice.

When we stood close to the hiding place of their chicks (without hand-

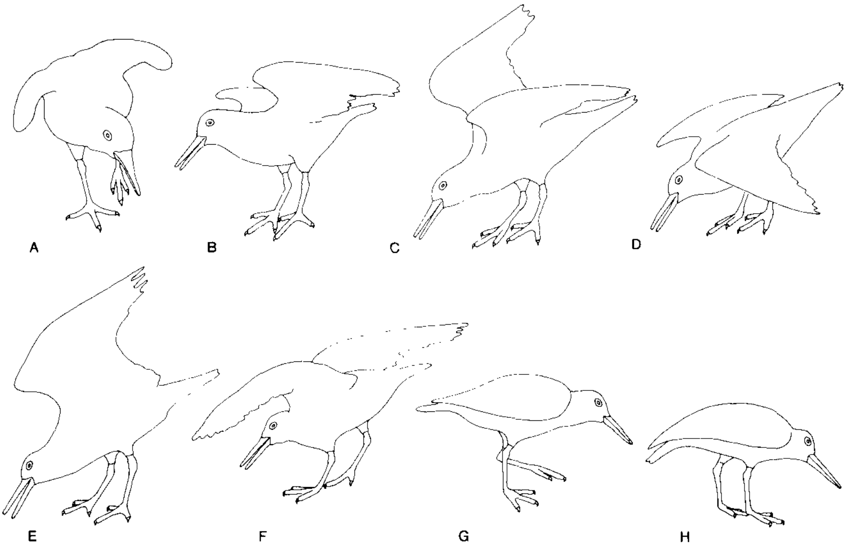

FIG. 4. Behavior of a female *H. moquini* (based on filmed sequence) in a distraction-lure display in defence of young in response to our presence. (See text for details.)

ling them), the birds gave lower-intensity distraction-lure displays with less pronounced tilting of the body and sometimes did not flap their wings. Although both birds of a pair performed this display they never did it simultaneously, and the female did the bulk of the displaying.

Both sexes also performed "broken-wing" displays (Deane 1944) in which one or both wings were extended and trailed on the ground as the bird ran ahead of us. Another form of this display involved a bird which crouched in a crevice and irregularly flapped its partly folded wings. In contrast to the distraction-lure displays these "injury-feigning" lure displays (Williamson 1952) were given without vocalizations.

Birds incubating eggs did not give the elaborate distraction displays described above, but instead both sexes performed repeated bouts of "false brooding" (Makkink 1942) away from the nest-site. One pair with pipped eggs performed both false brooding and brief broken-wing displays.

Butterfly flights.—Adult *H. moquini* were often observed in "butterfly flights" (Huxley and Montague 1925) when flying across occupied territories in the breeding season. Following a prolonged bout of piping on the ground, one pair followed a departing intruder with an aerial chase. On the return flight the leading bird switched suddenly to butterfly flight with characteristically slow, exaggerated wing beats. Although most displays were given by one bird, up to three presumed pairs were observed in group butterfly flights on Malgas Island in early January. In one example, the lead bird of a pair vocalized and performed butterfly flight above several territories, and in a return sweep both birds displayed. Another pair flew over and joined in with their butterfly flights, and eventually a third pair flew over and participated too. Since most birds on Malgas Island at this time of the year had young or eggs near hatching, these displaying birds were presumably failed breeders or newly formed pairs. On one occasion a bird ran slowly along the ground vocalizing with its wings raised high, and then took off and performed butterfly flight.

Fighting.—Fights occurred most often when birds were prospecting for mates and territories, or when piping displays failed to drive intruders from territories. Fighting usually consisted of charging with the bill thrust directly at the opponent's body. In some fights birds snatched at each other with partly opened bills, or grasped an opponent by the back of the neck and beat it with flapping wings while dragging it backwards. Fights were often followed by bobbing and displacement or "false feeding." Bouts of fighting were sometimes interrupted when one of the combatants adopted the "pseudo-sleeping" posture (Makkink 1942) by turning its head horizontally through 180° and hiding the bill in the scapulars. Unlike true sleeping, the eyes were kept open and focussed on the opponent when this posture was maintained. The pseudo-sleeping attitude was adopted frequently by both members of a pair when one of them returned to the territory after an absence. This posture may function to prevent aggressive interaction between members of a pair during a brief recognition period because we never saw attacks on birds adopting it.

VOCALIZATIONS

Piping.—Because piping displays usually involved several calling birds it was not always possible to identify which calls were made by particular individuals. However, we recorded a short segment of piping by one bird of a pair which was given in response to another bird which was emitting similar vocalizations during a distraction-lure display. The piping bird began with short "chip" calls which ascended in frequency, and then it switched to repeated units arranged in rising and falling couplets of lower and higher frequency calls (upper panel, Fig. 5). The bird progressively increased the loudness and frequency range of the first call in the couplets until they were subequal, and then it delivered a series of 11 long calls followed by a trill of "*pic*" calls called which ended the display (lower two panels, Fig. 5).

In longer displays, adult *H. moquini* cycled through this basic sequence of calls many times, though sometimes the beginning or concluding phrases of short notes were shortened considerably or even omitted. When

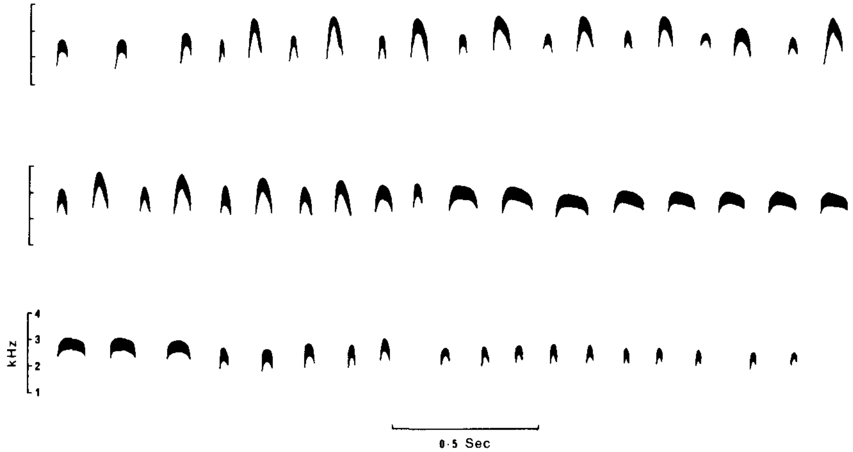

FIG. 5. Ground piping vocalizations given by one bird of a pair of *H. moquini.* Only the fundamental frequency of each call is shown.

both birds of a pair were piping together their sequences of calls were rarely similar. In several mutual displays we noted a tendency for the long calls of one bird to be followed by the long calls of its mate, but our samples are too small to test whether this resulted from synchronization or chance.

Distraction-lure vocalizations.—Three examples of the vocalizations accompanying the distraction-lure display are shown in Fig. 6. The major feature which distinguishes these vocalizations from those given in true piping is the rapid rate of repetition of calls. Two distinctive kinds of distraction-lure vocalizations were discernible in our recordings. In one kind the calls were short "*pics*" which usually graded into bi-peaked notes (Fig. 6A,B). These vocalizations are clearly composed of strings of alarm calls normally delivered at a much slower rate (cf. Fig. 7D and Fig. 8E–G). In the other kind of distraction-lure vocalization, which was most common, the calls are composed of regularly repeated couplets with alternating low and high frequency peaks (Fig. 6C), almost identical in arrangement to the second segment in piping (cf. Fig. 5).

The two kinds of distraction-lure vocalizations may reflect different motivational intensities of the displaying birds. The "alarm" kind of vocalizations in the two upper panels (Figs. 6A,B) were given when we were holding chicks in full view of their parents (high intensity), whereas the vocalizations in the lower panel (Fig. 6C) were given when we were standing near the rocks under which the chicks were hidden (lower in-

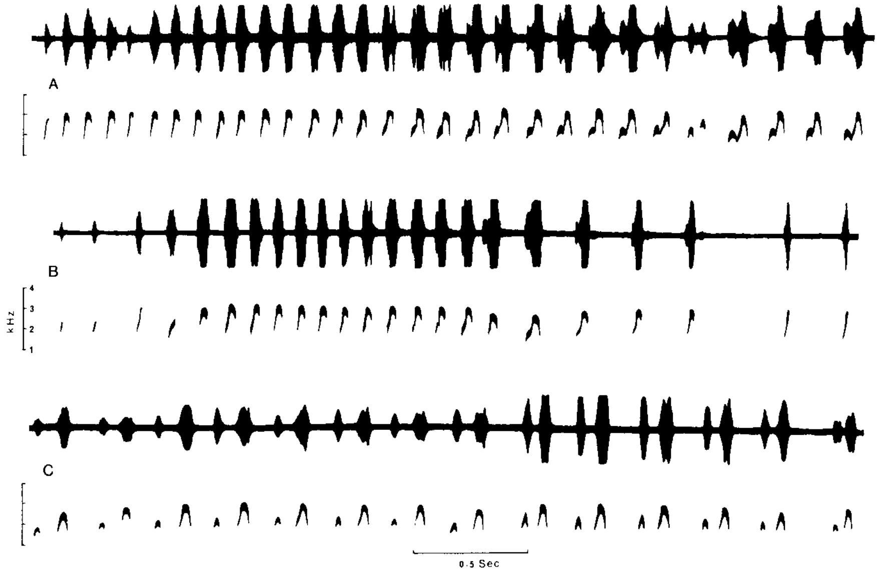

FIG. 6. Segments of distraction-lure display vocalizations of three different *H. moquini.* High intensity displays were given in response to chick distress calls (A,B), and low intensity forms were given when observers were near the hiding place of chicks (C). Only the fundamental frequency of each call is shown, with corresponding amplitude envelopes above.

tensity). Both sexes gave these vocalizations when attempting to lure us away from their chicks, although only one bird performed the display and vocalized at a particular time.

Alarm calls.—Hand-held chicks gave distress calls which varied with their age. Young chicks (ca 7–10 days old) gave spasmodic bursts of brief calls of similar frequency (Fig. 7A), but older chicks gave a variety of more complex calls involving rapid changes in frequency (Fig. 7B). Parents responded to these distress calls either with distraction piping or by emitting several different types of alarm calls. One bird gave trios of calls each of which began with a short chip followed by two long alarm calls (Fig. 7C), another gave complex two-part calls with different durations and frequency peaks (Fig. 7D), and other birds gave short *pic* calls which sometimes were emitted in pairs (Fig. 8E–G). Birds with eggs gave paired calls in which a short low frequency "chip" was followed by a longer and louder alarm call with a higher frequency peak (Fig. 8C–D). Both birds of a pair gave the same range of alarm calls and thus it was not possible to distinguish the sexes by their calls.

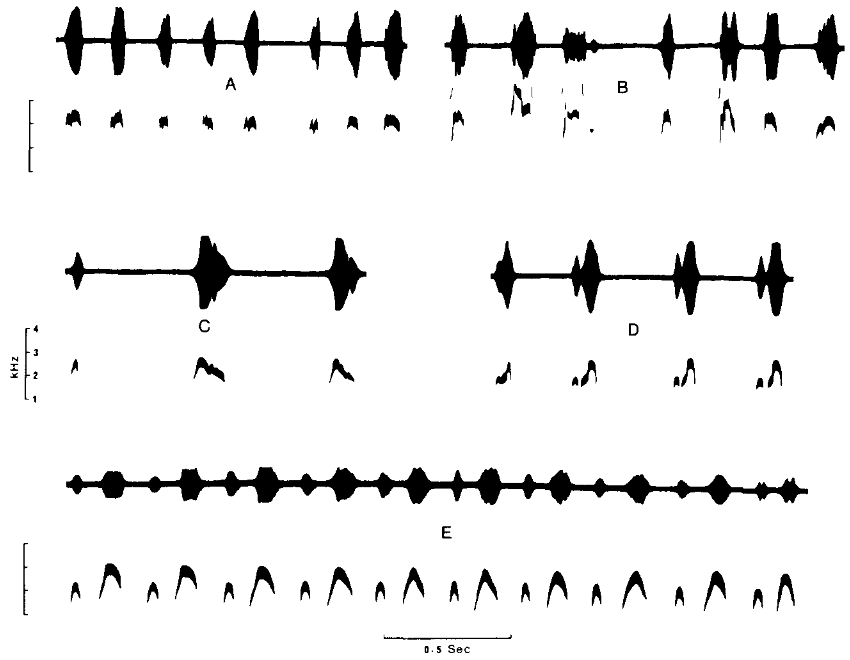

FIG. 7. Distress calls of chicks of *H. moquini* (A,B), alarm calls of adults given in response (C,D), and a segment of butterfly flight calls by an adult *H. moquini* (E). Only the fundamental frequency of each call is shown, with corresponding amplitude envelopes above.

Flight calls.—One adult *H. moquini* gave distinctive frequency and amplitude-modulated long calls when in flight (Fig. 8A). These calls are very similar to the *hueep* calls of New World species of oystercatchers (Miller and Baker 1980) which are given by pairs or single birds in flight, or by birds about to takeoff (Fig. 8B).

Birds performing butterfly flights often emitted vocalizations similar to those in the common form of the distraction-lure display. As in the latter, the calls are arranged in regularly repeated couplets of low and high frequency (Fig. 7E). The butterfly flight calls span a greater frequency range and are delivered at a slower tempo than their display-lure counterparts (cf. Fig. 6C). The slower tempo of the butterfly flight calls approximates the slow beat of the wings.

DISCUSSION

The behavioral and vocal repertoires of the African Black Oystercatcher are similar to those of other members of the Haematopodidae (except the

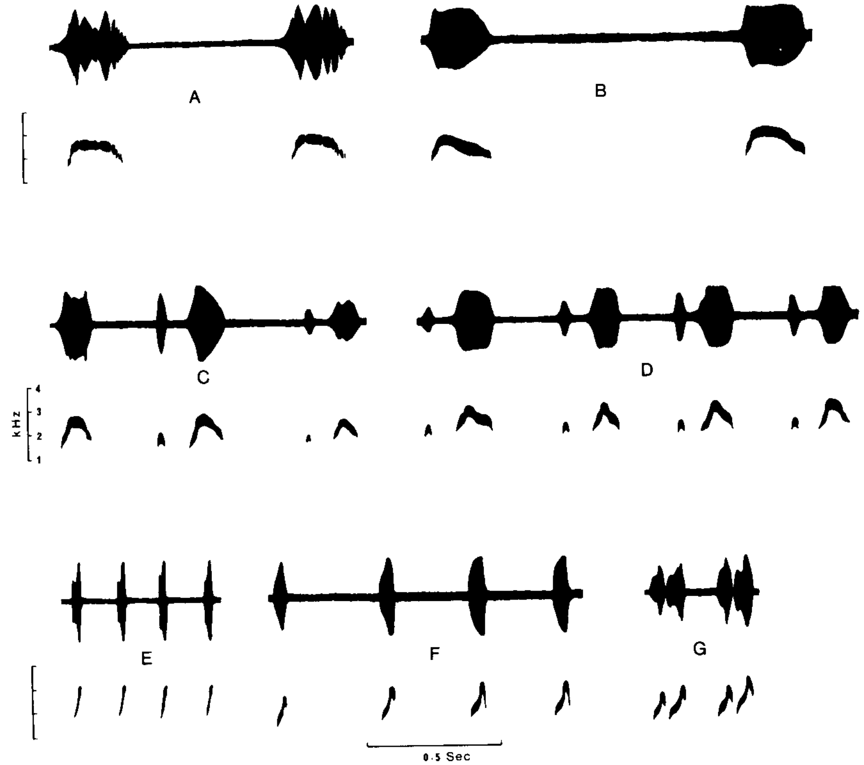

FIG. 8. *Hueep* flight calls (A,B), and alarm calls of adult *H. moquini* with eggs (C,D), and young (E,G). Only the fundamental frequency of each call is shown, with corresponding amplitude envelopes above.

aberrant Magellanic Oystercatcher [*H. leucopodus*]), and further support the contention that the Haematopodidae are an evolutionarily conservative group (Miller and Baker 1980). Despite this conservatism, *H. moquini* can be distinguished from other species of oystercatchers in specific aspects of its displays. The pre-copulatory display by the female appears to differ in *H. moquini* and the European Oystercatcher (*H. ostralegus*). In the latter the female assumes a passive posture while elevating the tail-end of the body (Makkink 1942), but in *H. moquini* the female appears only to crouch horizontally (Hall 1959, this study). Conversely, the "stealthy" approach of the male appears identical to that described for *H. ostralegus* (Huxley and Montague 1925, Makkink 1942).

Postures adopted by *H. moquini* during piping displays on the ground and in the air are very similar to those used by *H. ostralegus*. Both species perform parallel runs in which the birds arch their necks downward and hold their bills vertically. All species of oystercatchers in the New World (forms with yellow irides and pale flesh-colored legs) raise the tail vertically (*H. leucopodus*) or obliquely (Blackish Oystercatcher [*H. ater*], American Oystercatcher [*H. palliatus*], and Black Oystercatcher [*H. bachmani*]) during the piping display (Kilham 1980, Miller and Baker 1980), but all Old World taxa (forms with scarlet irides and coral pink legs) hold their tails horizontally (Rittinghaus 1964; Glutz von Blotzheim et al. 1975, fig. 9; pers. obs.). Tail-raising is not an invariable component of piping in *H. palliatus* and *H. bachmani,* however, and is usually of short duration when it does occur.

The distraction displays of all species of oystercatchers need to be studied in more detail before substantive conclusions can be drawn about the systematic value of any variations. Nevertheless, it is already clear that the distraction displays of *H. moquini* closely resemble homologues in *H. ostralegus.* Both species distract potential predators with the same range of behaviors including false brooding, rodent runs, injury-feigning and distraction-lure displays. The form of the distraction-lure display in *H. moquini* is probably unique to the species. The homologous display in *H. ostralegus* apparently is given silently (Williamson 1943, 1950; but see Cramp et al. 1983 for a report of "unspecified piping calls" during this display) and does not involve the striking forward slanted posture or alternating erection and depression of the tail seen in *H. moquini.*

Butterfly flights in *H. moquini* are most often performed above territories in the breeding season when birds are prospecting for mates or breeding sites. Although the interpretation of this display in other species of oystercatchers has been problematical (see Cramp et al. 1983), most of the confusion seems to have stemmed from its use as a displacement activity, and this has obscured its principal function as an advertising or display flight. All species of oystercatchers perform butterfly flights (pers. obs.), and although the accompanying calls have only been studied spectrographically in *H. moquini,* the phonetic descriptions of these calls in *H. ostralegus* (Dircksen 1932, Cramp et al. 1983) strongly suggest their similarity.

Spectrographic analysis of the vocalizations of *H. moquini* has revealed that this species has a limited number of calls which have obvious counterparts in other species (see Miller and Baker 1980, and Cramp et al. 1983). In the New World *H. ater, H. palliatus,* and *H. leucopodus,* the piping vocalizations of each species are very similar to their respective alarm calls, suggesting that piping is a highly ritualized form of these calls (Miller and Baker 1980). In *H. moquini,* however, the introductory and ending trills of piping resemble some alarm calls, and the couplets of low and high frequency notes in the second phrase are similar to the distraction-lure vocalizations.

The ground piping vocalizations of *H. moquini* are structurally distinct from those of *H. ater, H. palliatus,* and *H. leucopodus.* The latter species has unique narrow band vocalizations of almost constant frequency, whereas *H. palliatus* and *H. ater* have briefer wide band calls of varying frequencies (Miller and Baker 1980). Although the piping vocalizations of *H. moquini* are wide band and involve frequency shifts, their morphology is quite different from those of the New World species (cf. Fig. 5 this study and figs. 9–11 in Miller and Baker 1980). The piping calls of *H. moquini* are more similar to those of the Old World *H. ostralegus* than to the New World species (cf. call II in Cramp et al. 1983).

The vocalizations emitted during distraction-lure displays may be unique to *H. moquini,* although further sampling of calls of other species is required to substantiate this point. The close similarity of these calls to the second phrase in piping suggests that they have become ritualized in the distraction-lure display, and possibly in a slower and enhanced form in butterfly flight. Williamson (1952) argued that the distraction-lure display of *H. ostralegus* has evolved as a terrestrial modification of displacement butterfly flight. The close similarity of the vocalizations emitted during these displays in *H. moquini* lends support to this interpretation.

The alarm calls of all species of oystercatchers thus far studied are similar except in *H. leucopodus.* Most of the alarm calls of *H. moquini* are very similar to those of *H. ater, H. palliatus,* and *H. ostralegus* (cf. Figs. 7–8 this study, fig. 7 in Miller and Baker 1980, fig. 8A,B in Miller 1984, and calls V and VI in Cramp et al. 1983). In contrast to the New World species, however, both *H. moquini* and *H. ostralegus* have incorporated fewer of these types of alarm calls in their respective piping displays.

The *hueep* flight calls of *H. moquini* are almost identical to those of *H. ostralegus* (cf. Fig. 7A–B this study and calls I and II in Cramp et al. 1983). *Hueep* calls of *H. ater* and *H. palliatus* are longer and span smaller frequency ranges, thus distinguishing the New and Old World species.

While it is clear that further studies of oystercatchers are required to fully comprehend the evolution of display behavior in the Haematopodidae, nevertheless some useful conclusions can be drawn from this and earlier studies. The behavior and vocalizations of the African Black Oystercatcher strongly support its close affinity with the European Oystercatcher, but differences between them appear species-specific. The systematic value of similarties and differences in displays among oystercatcher species can best be assessed within a phylogenetic framework (Hennig

1966) which requires outgroup comparisons to determine whether character states are primitive or derived. Although Maclean (1972) pointed out problems of convergence and parallelism in display postures of Charadrii, detailed phylogenetic analysis not only can identify these problems but also can suggest which characters are useful in assessing relationships of taxa. Recent work using this approach on aerial displays of some species of Calidridinae has yielded very promising results (Miller 1983 a, b), confirming an earlier prediction that the systematic value of acoustic displays would be greatest in taxa using stereotyped sounds in long-distance communication and with little sound-learning (Mundinger 1979). These findings point up the need for broad comparative surveys of the behavior and vocalizations of shorebirds.

SUMMARY

The behavior and vocalizations of the African Black Oystercatcher (*Haematopus moquini*) were studied at Marcus and Malgas Islands in the southwestern Cape Province, South Africa. The behavioral and vocal repertoires of this species are broadly similar to other congeners, suggesting that the Haematopodidae are an evolutionarily conservative group. The African Black Oystercatcher has close affinity with the European Oystercatcher (*H. ostralegus*), based on the similarity of their piping postures, most distraction displays, alarm calls, and flight calls. These two species can be distinguished by differences in the pre-copulatory display of the female, the distraction-lure display, and possibly in piping vocalizations and butterfly flight calls. Assessment of the systematic value of these similarities and differences will depend on a future phylogenetic analysis with outgroup comparisons to determine character state polarities, and this in turn should encourage workers to attempt broad surveys of the behavior and vocalizations of shorebirds.

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CORRIGENDA 96:338 (1984)

P. 338, line 8 should read *Dendragapus canadensis*; lines 21–22 should read: . . . contradicts the text. Furthermore, I question the validity of placing the Spruce and Sharp-winged (*D. falcipennis*) grouse closer to the Blue Grouse. . . .