A comparative study of the breeding behaviour of the Augur Buzzard, Buteo augur, in two different land-use areas in southern Lake Naivasha, Kenya

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A comparative study of the breeding behaviour of the Augur Buzzard *Buteo augur* was made in two contrasting areas on the southern side of Lake Naivasha, Kenya. Hell's Gate National Park represented a natural site, and the lake environs an agricultural site. Locations of adult birds and their activity time budget during the breeding cycle were studied from April to October 1995. Factors influencing prey delivery and nestling feeding rates, and intra/inter-specific interactions were given special attention. Augur Buzzard pairs in the lake environs spent more time caring for chicks than their counterparts in Hell's Gate. This was apparent in the increased maternal care and paternal foraging which resulted in larger broods and more prey deliveries to nests respectively. Prey and biomass delivery rates to nests showed an increasing trend as the nestling period progressed. This was significant in the lake environs where brood sizes were larger than in Hell's Gate. Overall nestling feeding rates were also significantly greater in the lake environs than in Hell's Gate. Augur Buzzards in Hell's Gate spent significantly more time interacting with conspecifics and other species compared to those in the lake environs. We suggest that reduced predation pressure from conspecifics and other raptors in the lake environs as a result of lower inter/intra-specific interactions enabled Augur Buzzards to maximise provisioning of their young hence potentially increasing productivity.

Introduction

The Augur Buzzard *Buteo augur* is one of Kenya's most frequently seen birds of prey, inhabiting highlands, open moorlands, mountains, forest glades, inland cliffs and cultivated areas. Its distribution in Kenya ranges from the shores of Lake Victoria, across the eastern Rift Valley into the Tsavo plains before veering south into Tanzania (Lewis and Pomeroy 1989). Little information exists about the biology and ecology of the species (Virani 1999; Virani and Watson 1998). In East Africa, the Augur Buzzard is considered vulnerable to extensive afforestation of grassland habitat, or to lowered carrying capacity through overgrazing (Muhweezi 1990). The species mainly nests on cliff ledges and tall trees but adapts well to human settlement and extends onto grasslands using small exotic plantations for nesting and roosting (del Hoyo *et al.* 1994).

This paper examines the breeding behaviour of a population of adult Augur Buzzards in two different land-use areas. In the first, Augur Buzzards are resident in a National Park, where they nest on cliff ledges and exploit a wide prey base (beetles, birds, rodents and small mammals) (Virani 1999). In the second, they inhabit intensively farmed agricultural areas adjacent to the Park, where they nest in groves of tall *Acacia xanthophloea* trees and feed almost exclusively on rodents (Virani 1999). This paper tests the hypothesis that different land-uses necessitate different parental behaviours resulting in differences in breeding performance and parental survival.

Study areas and methods

The study was conducted in the southern Lake Naivasha area (0°45'S and 36°20'E), in the eastern Rift Valley of Kenya at an altitude of 1 890m (Figure 1). The two different land-use areas used as study sites were Hell's Gate National Park (hereafter referred to as Hell's Gate) and the lake environs (the area between the lake shore and outside Hell's Gate). The average rainfall in the area is less than 500mm per year (Ambrose 1984). Hell's Gate is located about 2km south of Lake Naivasha and covers an area of about 6 825ha. The main feature of Hell's Gate is the Ol-Njorowa gorge consisting of steep vertical cliffs. The vegetation is mainly scrubland dominated by an association of Tarchonanthus camphoratus and Acacia drepanolobium both of which rarely exceed 4m in height, and open grasslands dominated by Digitaria milanjiana. The upland grasslands that occur on the cliff scree slopes and on cliff tops are dominated by tussock forming grasses. Characteristic trees include Cussonia spicata, Schefflera abyssinica and Euphorbia magnicapsular. Since Hell's Gate is a protected area, the land-use activities are recreational. The lake environs included the area immediately surrounding Hell's Gate as well as the area inland from the lake's southern and western shores (Figure 1). Much of the lakeshore is fringed by papyrus Cyperus papyrus while the area immediately behind the shoreline has a thin band of closed canopy Acacia xanthophloea woodland with trees up to 35m tall. This woodland



Figure 1: The core study area in the southern Lake Naivasha area of Kenya.

tends to open up further into human-modified open canopy *Acacia* woodland pastures. Other tree species include *Euphorbia* candelabra and *Eucalyptus* sp. The grasslands consist mainly of *Setaria* spp which grades into the *Tarchonanthus camphoratus* bushland. The land-use patterns in the lake environs vary from intensive to moderate horticulture and cattle grazing, to large and small-scale human settlements.

Breeding behaviour data were collected between April and October 1995. The breeding cycle was divided into periods characterised by specific breeding stages – incubation, early nestling (downy nestling <c. 25 days old) and late nestling period (brown feathered nestling, >c. 25 days old). Four-hour watches of visually accessible nests were conducted for a total of 8 nesting attempts (4 in Hell's Gate and 4 in the lake environs) from 8 pairs of Augur Buzzards (Figure 2). Nest observations were made on a systematic basis but also influenced by availability (as well as visual accessibility) of active nests. Nest searches were conducted by intensively watching Augur Buzzard pairs for evidence of breeding activity such as carrying of nesting material or prey to nest, courtship behaviour and territorial displays. The 8 nests were observed on a rotational basis at different times



Figure 2: Location of nests of 8 pairs of Augur Buzzards observed for breeding behaviour in the two study areas.

of the day. A "day" was divided into three time sessions: from 06h30–10h30, from 10h30–14h30 and from 14h30–18h30. A 20–60 x spotting scope, plus a 10 x 50 pair of binoculars were used to observe breeding activity, while the 10 minute interval sampling method (Altmann 1974) was used to record Augur Buzzard activity and location with respect to the nest. We sat in a chairs placed usually under a tree not less than 200m from a nest. From experience, our presence during observation sessions did not appear to have any interference on parental breeding behaviour. The only possible source of interference during the observation sessions would have been that the tree under which we were seated, was not used as a perch. Each session comprised the following:

We usually arrived at the nest site at least 15 minutes prior to the start of the session and thoroughly searched for the location and activity of each of the adults;

At the start of a session and every 10 minutes thereafter, the location (with respect to the nest) and activity of both adults were recorded (Altmann 1974);

All "events" that occurred between each 10-minute data point were also recorded. These included territorial displays, interactions with other species, hunting attempts and prey



Figure 3: (a) Proportion of time spent at various distances from the nest by male and female Augur Buzzards in Hell's Gate (HG) and the lake environs (LE) during the incubation (n = 78 hrs), early nestling (n = 144 hrs) and late nestling (n = 124 hrs) stages. (b) Proportion of time spent by male and female Augur Buzzards in various activities in Hell's Gate (HG) and the lake environs (LE) during the incubation (n = 78 hrs), early nestling (n = 144 hrs) and the lake environs (LE) during the incubation (n = 78 hrs), early nestling (n = 144 hrs) and late nestling (n = 124 hrs) and late nestling

deliveries. Biomass of each identifiable prey item delivered to nests was estimated (Kingdon 1974).

A total of 346 hours was spent observing 8 Augur Buzzard nests (4 in Hell's Gate and 4 in the lake environs) during different stages of the breeding cycle. The male and female of each of the 8 pairs observed were readily distinguishable by either colour morph, "window" marks in their mid-secondary feathers, plumage, and/or rings.

The proportion of time spent in each activity by each adult Augur Buzzard in relation to the distance from the nest was calculated and Mann-Whitney analysis was used to test for differences in time budget. Breeding data were categorised by site (Hell's Gate and lake environs), sex (male and female) and breeding stage (incubation, early nestling and late nestling).

Standard ANOVA was used to test for within site differences in prey delivery and prey biomass rates, and aggressive interactions in relation to time of the day, breeding stage and brood size. A t-test was used to test for differences in feeding rates to chicks.

Results

The density of Augur Buzzards was 0.28 pairs per km2 in Hell's Gate and 0.23 pairs per km2 in the lake environs. The mean nearest-neighbour distance between pairs was 1.29 km in Hell's Gate (n = 14, se = 0.09, range = 0.81-1.90) and 1.62km in the lake environs (n = 19, se = 0.14, range = 0.66-2.71). The mean nearest-neighbour distances between the two areas were not significantly different (p > 0.05).

Three of the 4 nests observed in Hell's Gate were on cliffs (H1, H2A, H6A) while the fourth (H5A) was on a Euphorbia magnicapsular tree. In the lake environs, 3 of the 4 nests were on Acacia xanthophloea trees (R1, K1, K3) while the fourth was on an E. magnicapsular tree (S5). In Hell's Gate, 2 of the 4 nests (H1, H6A) failed during the incubation period but the parents re-laid within a period of two weeks. Nest H1 failed, apparently because rock climbers were too close to the nest, resulting in the eggs being unattended for a long period, while the eggs of nest H6A were depredated by baboons. All 4 pairs in Hell's Gate plus two pairs in the lake environs (R1 and K3) successfully fledged one chick each while pairs K1 and S5 successfully fledged two chicks each. Siblicide behaviour was observed only in one nest (R1), which resulted in the death of a ten-day old chick. The overall reproductive success wasone chick per breeding pair per year for Hell's Gate and 1.5 chicks per breeding pair per year for the lake environs (n = 8 nests).

Location and activity time budget during the breeding cycle

Incubation stage

During incubation, food exchanges occurred without intersexual aggression. Males with prey initiated the changeover by either calling from a perch within sight of the nest or perching on the nest itself. Females usually took the prey and flew away from the nest to feed. The male typically initiated incubation once the female left the nest and remained on the nest until the female returned. Female Augur Buzzards from the lake environs spent 88% (se = 5.9) of their time at the nest compared with females from Hell's Gate, who spent only 60.7% (se = 8.29). This difference was "statistically significant at p = 0.051 level" (Figure 3a). Male Augur Buzzards from Hell's Gate spent significantly more time (34.9% se = 8.02) at the nest during the incubation period than males from the lake environs (8.8% se = 5.06) (p < 0.05) (Figure 3a). While at the nest, females from the lake environs spent significantly more time attending to eggs (p < 0.05) than those from Hell's Gate, which spent more time perched close to their nests (Figure 3b). Males from Hell's Gate spent significantly more time (34.4% se = 8.15) incubating compared to those from the lake environs (7.8% se = 5.18) (Figure 3b) (p < 0.05).

Early nestling stage

During the early nestling period, prey exchanges between adults always occurred at the nest. If the female was not on the nest when the male arrived, she flew immediately to it to take the prey from the male with her bill or talons. Alternatively, the male would simply drop the prey on the nest and fly off. Females from Hell's Gate spent more time perched close (<200m) to their nests than those from the lake environs, although the difference was not significant (NS) (Figure 3a). Males from Hell's Gate spent more time attending to chicks than their counterparts from the lake environs, although this difference was not significant (NS) (Figure 3b).



Figure 4: Prey delivery rates (a) and biomass of prey delivered per hour (b) to nests in Hell's Gate (HG) and the lake environs (LE) at different times of the day (bars represent standard errors)

Late nestling stage

Females from the lake environs spent significantly more time (12.3% se = 3.33) at the nest compared to those from Hell's Gate (4.4% se = 2.84) (p < 0.05). Male Augur Buzzards from Hell's Gate spent significantly more time (15.7% se = 4.56) perched closer to their nest than those from the lake environs (3.9% se = 2.08) (p < 0.01) (Figure 3a). Females from the lake environs spent significantly more of their time (6.2% se = 2.94) attending to chicks at the nest as opposed to those from Hell's Gate (0.1% se = 0.1) (p < 0.01) (Figure 3b). There were no significant differences between the respective males and females of both areas in the amount of time spent feeding young, eating and flying (NS).

Factors influencing prey delivery rates *Time of the day*

Time of the day did not significantly influence prey deliveries to nests in either Hell's Gate (NS) or the lake environs (NS), although most prey items were delivered between 12h30 and 14h30 (Figure 4). In Hell's Gate, the general trend was an increase in prey deliveries in the first two hours after dawn, followed by a decrease, and then an increase that peaked between 12h30 and 14h30 (Figure 4). Prey delivery rates in Hell's Gate waned after 14h30 (Figure 4). In the lake environs, the general trend was a gradual increase in prey delivery rates that peaked between 12h30 and 14h30 followed by a gradual decrease (Figure 4). In terms of biomass, deliveries to nests showed the same trends as with prey deliveries and did not significantly differ at different times of the day in either Hell's Gate (NS) or the lake environs (NS) (Figure 4).

Breeding stage

In Hell's Gate, prey delivery rates to nests did not significantly differ between the various breeding stages, although an increasing trend was evident as the breeding cycle progressed (NS) (Figure 5). In the lake environs, prey delivery rates to the nest were significantly greater during the late nestling stage compared to the incubation and early nestling stage (p < 0.001) (Figure 5). When breeding stages were compared between the two sites, there were no significant differences in the prey delivery rates to nests during both the incubation (NS) and early nestling stage (NS). However, prey delivery rates to nests in the lake environs, during the late nestling stage were significantly greater than those in Hell's Gate (p < 0.01).

Biomass deliveries to nests also showed the same trends as prey deliveries. In Hell's Gate, biomass delivered to nests did not significantly differ during the various breed-





Figure 5: Prey delivery rates (a) and biomass of prey delivered per hour (b) to nests in Hell's Gate (HG) and the lake environs (LE) during different breeding stages (bars represent standard errors)

Figure 6: Prey delivery rates (a) and biomass of prey delivered per hour (b) to nests with different brood sizes in Hell's Gate (HG) (1 chick per nest; n = 4) and the lake environs (LE) (2 chicks per nest; n = 2) during different breeding stages (bars represent standard errors)

ing stages (NS) (Figure 5). However in the lake environs, biomass delivered to nests was significantly greater during the late nestling stage compared to the incubation and early nestling stages (p < 0.001) (Figure 5). Between the two sites, biomass delivered to nests was not significantly different during the incubation (NS) and early nestling stage (NS) (Figure 5). However, biomass delivered to nests in the lake environs during the late nestling stage was significantly greater than in Hell's Gate (p < 0.01) (Figure 5).

Brood size

Prey delivery rates to nests with different brood sizes in Hell's Gate and the lake environs did not significantly differ during the incubation (NS) and the early nestling period (NS). However, during the late nestling stage, prey delivery rates to nests in the lake environs were significantly greater than in Hell's Gate (p < 0.01) (Figure 6). Also in the lake environs, nests with single chicks had significantly greater prey delivery rates compared to those in Hell's Gate during the late nestling period (p < 0.05).

Biomass delivered to nests with different brood sizes showed same trends as with prey deliveries (Figure 6). In the lake environs, biomass delivered to nests that contained two chicks was significantly greater during the late nestling stage compared to the incubation and early nestling stages (p < 0.05) (Figure 6).

Factors influencing nestling feeding rates

The rate at which Augur Buzzards fed their nestlings was significantly greater in the lake environs than in Hell's Gate (p < 0.05). The feeding rate throughout the breeding cycle of Augur Buzzards in the lake environs was about twice as high as that of Hells Gate (Hell's Gate: 0.28 [se = 0.05] feeding bouts per hour; lake environs: 0.13 [se = 0.04] feeding bouts per hour). Within both areas, although feeding rates were more frequent during the earlier than later stages of the breeding cycle (Figure 7), these results were not significant-



Figure 7: Feeding rates of freshly delivered items to Augur Buzzard nestlings by parents in Hell's Gate (HG) and the lake environs (LE) during the early and late nestling stages (bars represent standard errors)

ly different (NS).

Nests with two chicks had a feeding rate (0.35 [se = 0.07] feeding bouts per hour) that was almost three times higher compared to those with single chicks (0.13 [se = 0.03] feeding bouts per hour), a highly significant difference (p < 0.001).

Intra and inter-specific interactions

Breeding Augur Buzzards showed two types of behavioural patterns in response to the presence of conspecifics or other species in their territories. These were territorial displays and aggressive interactions. Territorial displays involved both individuals of a pair circling close together above their territory, with legs dangling downwards, whilst at the same time calling. Aggressive interactions involved one or both individuals of a pair, flying towards a potential intruder (or intruders). This was followed by one (or both) individual 'dive-bombing' the intruder (sometimes grappling talons or making contact) and chasing it away from the pair's territory. Calling did not usually take place during aggressive interactions.

The majority of territorial displays in both Hell's Gate and the lake environs occurred in response to other Augur Buzzards intruding in to occupied territories. In Hell's Gate, this was 42% of the territorial displays, while the rest were in response to adjacent Augur Buzzard pairs (14%), immature Augur Buzzards (5%), other raptors (15%) and baboons (10%) (n = 46 territorial displays). In the lake environs, 59% of the territorial displays were in response to intruding Augur Buzzards while during the rest of the displays, no species were seen within the occupied territories (n = 27 territorial displays).

In Hell's Gate, aggressive interactions took place against other raptors – eagles (30%), vultures (30%), conspecifics (18%), as well as baboons (7%) (n = 72 aggressive interactions). In the lake environs, aggressive interactions took place mainly against the African Fish Eagle *Haliaeetus vocif*-



Figure 8: Aggressive interaction rates with conspecifics and other animals at different time phases of the day in Hell's Gate (HG) and the lake environs (LE) (bars represent standard errors)



Figure 9: Aggressive interaction rates with conspecifics and other animals during different breeding stages in Hell's Gate (HG) and the lake environs (LE) (bars represent standard errors)

er (51%), conspecifics (21%) and serval cats *Leptailurus serval* (14%) (n = 37 aggressive interactions).

The mean aggressive interaction rate (AI rate) for Hell's Gate (0.38 [se = 0.05] interactions per hour) was twice as high and significantly greater than the rate for the lake environs (0.18 [se = 0.04] interactions per hour) (p < 0.01). There were no significant differences in the mean AI rate between the different time phases of the day in Hell's Gate and the lake environs (NS). In Hell's Gate, mean AI rates were high throughout the day with peak interactions occurring between 12h30 and 14h30 (Figure 8). In the lake environs, mean AI rates were relatively lower and mainly occurred between 10h30 and 16h30 (Figure 8).

In Hell's Gate, there was no significant difference in the mean AI rates between the different breeding stages (Figure 9). However, in the lake environs, the mean AI rate during the late nestling stage was significantly greater than AI rates during the incubation and early nestling stage (p < 0.05) (Figure 9).

Discussion

Breeding behaviour

Augur Buzzards in the lake environs nested in trees and were more productive than those in Hell's Gate. Females in the lake environs attended eggs more often, spent more time with large nestlings, had more prey and biomass deliveries to nests, had higher feeding rates and spent less time defending territories against both conspecifics and other raptors. Males in Hell's Gate spent more time incubating (up to 4 times more), attending to nestlings and stayed close to nests during the nestling period. These breeding behavioural differences imply a functional response to habitat characteristics. Food quantity and quality, predation pressure, human disturbance (persecution and habitat alteration) and intra/inter specific interactions are all possible factors that can influence parental breeding behaviour. The proportion of incubation time spent by Augur Buzzard males in Hell's Gate compared closely with males of this species in the Matopos hills, Zimbabwe, which was 27% (Lendrum, 1979). Augur Buzzard males in the Impenetrable Forest, Uganda, spent 18% of their time incubating which was disproportionately low given that nests were left unattended for a similar proportion of time (Muhweezi 1990). The proportion of incubation time spent by Augur Buzzard females in Hell's Gate (61%) compared closely with both the Impenetrable Forest (65%) (Muhweezi 1990) and Matopos hills (66%) (Lendrum 1979).

Our data, plus available literature on Augur Buzzard incubation periods suggest that the incubation behaviour of Hell's Gate males is the norm and that of males in the lake environs is influenced by other factors. One explanation is that reduced predation pressure from baboons, ravens, crows and other raptors in the lake environs means that females can expend more energy raising chicks and less energy defending their territories against potential predators and/or intruders. Augur Buzzards in Hell's Gate spent more time interacting with conspecifics and other raptor species compared to those of the lake environs. This probably reflects a pattern determined by more predators in Hell's Gate than in the lake environs and not a function of either Augur Buzzard density (which is similar in both areas) or their diurnal cycle. Thiollay and Meyer (1978) attributed low breeding success in the African fish eagle in Uganda to high breeding densities associated with greater interactions between pairs. Increased inter and intra-specific interactions may also be construed as a sign of increased predation pressure. Lendrum (1979) reported high inter-specific interactions between Augur Buzzards and other large raptors in the Matopo hills where predation pressure was apparently high. Female raptors are usually associated with nest defence, and given that both Hell's Gate and the Matopo hills harbour a rich diversity of raptors (Gargett 1990; Lester 1991), it would be logical to suggest that males spend more time incubating in these areas because females are constantly on the alert to ward off potential predators and/or intruders. The paucity of inter-specific interactions in the lake environs implies that female Augur Buzzards can spend longer periods incubating, attending to chicks and feeding young, while males can spend more time hunting. Augur Buzzard pairs in the lake environs had larger brood sizes and higher productivity than those in Hell's Gate (Virani 1999). This could be attributable to greater maternal care (feeding rates, brooding, incubation) and paternal provisioning in the lake environs

Prey delivery rates and its correlates

Prey deliveries to nests were highest between 10h30 and 14h30 in both areas. Virani (1999) found that rodents were mainly delivered to nests between 10h30 and 16h30 and their foraging activity times coincided closely with the time prey were delivered to Augur Buzzard nests (Jarvis 1969; Kingdon 1974). The principal prey items of Augur Buzzards in Naivasha are mole-rats (Smeenk 1974; Kingdon 1974; Brown and Britton 1980; Virani 1999), and their activities outside their burrows are confined to between 10h00 and 19h00 (Jarvis 1973). Augur Buzzards are also a major pred-

ator of vlei rats Otomys angoniensis which spend long hours feeding but show no preference for particular time periods (Kingdon 1974). Virani (1999) found that vlei rats were mainly delivered to nests during the early and late afternoon periods. The time period of most prey deliveries to nests was comparable to that for Augur Buzzards in the Impenetrable Forest, where 76% of prey were delivered between 09h00 and 13h00 (Muhweezi 1990). Mountain Buzzards Buteo oreophilus in the Impenetrable Forest also delivered the majority of their prey to nests between 10h00 and 15h00 (Muhweezi 1990). Our data showed that peak prey delivery rates in both sites coincided with peak aggressive interaction rates. These were mainly conspecific territorial displays between adjacent pairs or intruders. This suggests a high level of territoriality and competition (against non-territory holding individuals) with the potential to affect reproductive success.

Prey deliveries and biomass to nests increased as the nestling period progressed. This was significant in the lake environs where there were also more chicks per nest than in Hell's Gate. In many studies of Peregrine Falcons Falco peregrinus, Marsh Harriers Circus aeruginosus., Ospreys Pandion haliaetus, Kestrels Falco tinnunculus and Sparrowhawks Accipiter nisus, the number of prey items and biomass increased during the nestling period, as the young grew, and differed between nests with various brood sizes (Tinbergen 1940, 1946; Enderson et al. 1973; Johanesson 1975; Green 1976). In Peregrine Falcons, male provisioning rates were positively correlated with brood size and fledging success, but that of females was unrelated to brood size, fledging success or male delivery rate (Olsen et al. 1998). In the Madagascar Buzzard Buteo brachypterus, prey delivery rates to nests did not significantly differ between the early and late nestling stages probably as a result of the birds being generalist feeders (Berkelman 1994). If Augur Buzzards in Hell's Gate were delivering larger prey, then prey delivery rates would be fewer. Our study found no evidence to show that biomass was different between the two sites (although it differed between different breeding stages and nests with different brood sizes). The differences in prey delivery and biomass could be attributable to abundance of prey in these areas (see Virani 1999). The greatest growth in wing and tail length in Augur Buzzard nestlings occurred between 21 and 42 days after hatching (Lendrum 1979) and therefore the nutritional requirements of chicks would be greatest between this period. Thus if a pair of Augur Buzzards have two chicks to feed during the late nestling period, then prey delivery and biomass rates to their nest will be significantly greater, as with the Augur Buzzards in the lake environs. More chicks per nest in the lake environs also meant that overall feeding rates there were significantly greater compared to Hell's Gate. Reduced aggressive interaction rates in the lake environs means that female Augur Buzzards can assist males in raising larger broods by helping to hunt. Larger broods in Peregrine Falcons were fed more regularly than smaller broods, and were fed at peak rate longer into the nestling period (Olsen et al. 1998). Feeding rates were more frequent during the early nestling stage, and suggests that early stage nestlings were more dependent on being fed by females. As nestlings grow older,

they begin to feed by themselves, thus leaving females more time to help males in hunting food.

Augur Buzzard pairs in the lake environs spent more time caring for chicks than their counterparts in Hell's Gate. This was shown by increased maternal care and paternal foraging which resulted in larger broods and more prey deliveries respectively. The factors responsible for these are reduced predation pressure and inter/intra-specific interactions.

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