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High Rates of Conspecific Brood Parasitism and Egg Rejection in Coots and Moorhens in Ephemeral Wetlands in Namibia

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Conspecific brood parasitism (CBP) is not as easy to detect as interspecific brood parasitism, but field studies that involve careful nest monitoring and behavioral observation during the laying period have indicated that CBP may be more common and widespread than previously thought (Yom-Tov 1980, Andersson 1984, MacWhirter 1989, Lyon 1993a). For example, relatively high levels of CBP have been found in American Coots (*Fulica americana;* Arnold 1987, Lyon 1993a) and Common Moorhens (*Gallinula chloropus;* Gibbons 1986, McRae 1995). In addition, the above species sometimes respond to parasitism by either deserting their nest (moorhens) or selectively burying the parasitic egg (coots). Presumably, these host responses evolved because of increased fitness costs resulting from attempting to raise parasitic offspring (Yom-Tov 1980, Andersson 1984).

We studied unmarked migratory populations of Red-knobbed Coots (*Fulica cristata*) and Lesser Moorhens (*Gallinula angulata*) in an ephemeral wetland in Namibia, Africa; CBP had not been previously recorded in either of these species. Yearly rainfall in the area is extremely variable and unpredictable, but when heavy rains occur and pans and surrounding grasslands become flooded, many wetland species of birds arrive within days of flooding (Hines 1993, Simmons et al. 1999). Wetland areas with a combination of deep water (>1 m) and vegetative cover are limited (R. Simmons pers. obs.); hence, the synchronized arrival and subsequent high density of birds may result in a shortage of available nesting sites. Nest predation is also thought to be high during years of heavy rainfall because of the presence of numerous egg predators such as monitors, snakes, and jackals (J. Mendelsohn pers. comm.). Shortages of nest sites and high rates of nest predation have been associated with increased frequency of CBP (Yom-Tov 1980, McRae 1997a).

The objectives of our study were to document rates and patterns of CBP in Red-knobbed Coots and Lesser Moorhens and to describe host responses to parasitism. We compared our data with those reported for coots and moorhens in northern temperate environments and discuss how ecological factors and behavioral constraints may have led to variation in host responses among these species.

Methods.—The study was conducted near Nyae Nyae pan, which is located 20 km south of the settlement of Tsumkwe, Bushmanland, in northeastern Namibia (ca. 20°15′S, 20°35′E). Nyae Nyae is the largest of a group of 13 alkaline pans that normally are dry except during periods of heavy rainfall. Grassy marshes (dominated by *Diplachne* spp.) surrounding the unvegetated pans are limited in size, and their period of inundation is highly variable both within and between years (Hines 1993). Our study area comprised two sites that were approximately 1 km apart. One was on the eastern edge of Nyae Nyae pan, where all of the coot nests and about one-quarter of the moorhen nests were located. The remaining moorhen nests were found at a similar site at the northwestern end of the pan.

Most fieldwork was conducted from 5 to 27 February 1997. Active nests were checked daily except for 15 to 17 February, when we were absent from the study area. Coots and moorhens require approximately 25 and 18 days, respectively, to incubate their eggs. Thus, complete data on hatching and fledging success were not obtained. We returned to the area from 17 to 22 March to conduct a second nest survey. Moorhens had finished nesting by that time, but coots continued to initiate new nests, although data collection was limited by the short time period.

Red-knobbed Coot nests are large and conspicuous, and we are confident that we found virtually all nests within our study area; however, Lesser Moorhen nests are smaller and more difficult to find. Once a moorhen nest was located, we searched a radius around the nest of about 50 m to try to locate all nests on adjacent territories. During nest visits, new eggs were numbered with an indelible marker. Any egg that was more than half buried in the nest cup was recorded as "buried" but was collected only after it had completely disappeared below the nest lining. All new nests were initially checked for buried eggs. Nests found with two or more eggs already in the clutch (excluding parasitic eggs; see below) were backdated to determine clutch initiation date by as-

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suming one egg was laid per day (Lyons 1993a, McRae and Burke 1996; see Results).

Parasitic eggs were identified in the field using two standard criteria (Arnold 1993; Lyon 1993a, b; McRae and Burke 1996; McRae 1997b): (1) the appearance of two new eggs in the nest on the same day, and (2) the appearance of a new egg in a nest more than two days after clutch completion. A third criterion was used to identify additional parasitic eggs in a "known" parasitized nest (i.e. as determined by criteria above): (3) any egg found buried in the nest that did not match the host's eggs in background color, spotting pattern, size, and shape was deemed parasitic. We felt justified in assuming that buried eggs that were different from a host's eggs were parasitic because 52% (n = 21) of known parasitic eggs of coots (using criteria 1 and 2) were subsequently buried, compared with only 3% (n = 144) of known host eggs (three of five of which were buried by the same pair in the same nest). Similarly, 43% (n = 7) of known parasitic eggs of moorhens were subsequently buried, compared with 0% (n = 29) of known host eggs.

When a female coot had completed her clutch, we placed all of the eggs in the nest, plus any that had been buried, on a flat board covered with black felt and took a photograph; the high rate of predation on moorhen nests precluded obtaining enough photos of their eggs and conducting the following analyses. Parasitic eggs were compared in the nest and on photographs and visually matched with eggs laid in other nests to determine whether parasitic females could be identified. Matching eggs laid in two different clutches using egg features has been used to identify parasitic females American Coots (Arnold 1993; Lyon 1993a, b). To determine whether the rejection or acceptance of foreign eggs in coot nests was related to how similar or different they were from the host eggs, slide transparencies of each clutch were examined and the similarity of host and parasitic eggs scored independently on a scale from 1 to 4: (1) "very similar" (within the range of variation shown in host eggs), (2) "moderately similar" (outside the range of variation in host eggs but still difficult to distinguish), (3) "moderately different" (outside the range of variation in host eggs and relatively easy to distinguish), and (4) "very different" (clearly distinct from host eggs). We then averaged our scores for each parasitic egg and categorized those with scores between 1 and 2 as "similar" and between 3 and 4 as "different." Eggs with average scores of 2.5 were eliminated from the analysis. Of 29 parasitic eggs, 69% received identical scores, and 31% differed by a score of 1; only two eggs (both from the same nest) received a mean score of 2.5.

Results.—Rain began falling in the area during the last week in December, and Nyae Nyae pan was full to capacity by mid-January (N. Berriman pers. comm.). A brief survey of the Nyae Nyae area on 26 January recorded few coots and moorhens and no nests (S. von Plato pers comm).

Backdating clutches of Red-knobbed Coots found during the first week of our nest surveys (begun 5 February) indicated that most of them (65%, n = 20) had been initiated during the previous six days. A significantly higher proportion of the clutches initiated in the first 2.5 weeks of the nesting period ("early nesting;" 11 of 15 nests) received at least one parasitic egg compared with the subsequent 2.5 weeks ("mid-nesting;" 1 of 15) or during a 2.5-week nesting period in March ("late nesting;" 6 of 12; $\chi^2 = 13.97$, df = 2, $P < 0.001$). Of the 47 known parasitic coot eggs, 64% were laid in the early nesting period, 4% during the mid-nesting period, and 32% during the late-nesting period. However, a large proportion of the late-nesting clutches either were complete (36%, n = 22) by the time our survey commenced on 17 March, or were incomplete (36%) by the time we left six days later. Therefore, estimates of parasitism rates during this period were less accurate compared with the early nesting period when egg-laying data were more complete and nests were checked daily. For the next section, we concentrate on the early nesting period to characterize the nature of parasitism in Red-knobbed Coots.

Early nesting hosts received from one to six parasitic eggs ($\bar{x}$ = 2.7 ± SE of 0.49, n = 11 nests). In five of the eight nests that received two or more parasitic eggs, all of the parasitic eggs matched each other, indicating that the same female probably laid them. In the remaining three nests, two different parasitic females were implicated; four of these six females also laid two to three parasitic eggs each. No coot nest was parasitized by two females on the same day.

Based on buried eggs, we estimated that only three female coots had parasitized host nests (16% of 30 parasitic eggs) before 7 February when our intensive nest surveys began. Between 7 and 13 February, when we checked all coots nests in the main study area daily, parasitic laying peaked on 9 February and declined thereafter, even though the number of potential host nests increased (Fig. 1). The number of parasitic eggs laid by individual females ranged from one to six ($\bar{x}$ = 2.1 ± 0.36, n = 15 females), and as far as we could tell parasites always laid in the same host nests. Most parasitic eggs (80%) were laid during the laying period of the hosts.

Female coots that were in the process of laying their own clutch were unlikely to be parasites given that females can lay no more than one egg a day, and that most hosts laid eggs in their own nests on consecutive days. Only three females skipped a day in their laying sequence between 7 and 13 of February. None of the parasitic coot eggs laid on a particular day during that period matched those of females that had skipped laying on the same day.

By matching eggs in the field, six female coots (63% of the 30 parasitic eggs) were identified as lay-

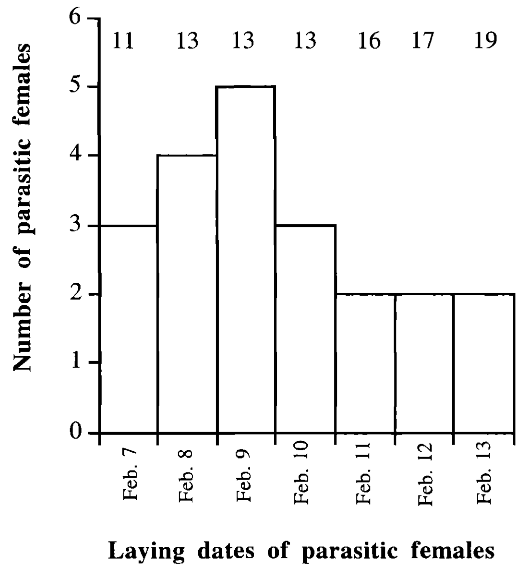

FIG. 1. The number of female Red-knobbed Coots that laid parasitically in the nests of conspecifics between 7 and 13 February 1997, when all nests within the main study site were checked daily. Numbers above the bars indicate the number of host nests available for parasitism.

ing parasitic eggs before commencing their own nests; one of these females nested in the early nesting period and the remaining five in mid-nesting period. The estimated time between laying parasitically and laying in one's own nest averaged 3.9 ± 1.5 days. Parasitic coots laid clutches in their own nests ($\bar{x}$ = 9.0 ± 0.32, n = 5) that were similar in size to those laid by nonparasitized coots at the same time ($\bar{x}$ = 9.4 ± 0.36, n = 12; Mann-Whitney U = 21.5, P = 0.35). Two other females (7% of parasitic eggs) each laid one parasitic egg immediately after their own nests were destroyed by flooding during the laying period. All eight of the parasitic female coots laid eggs in host nests that were only one (n = 6) or two (n = 2) territories from their own nests, and 18 of their 20 parasitic eggs were laid during the host's laying period.

We were unable to match five groups of parasitic eggs (30% of parasitic eggs) to any female coot on the study area. The timing of laying with respect to the host's laying period was unknown for three parasitic eggs in one of these groups. The remaining four unmatched groups of eggs (20% of parasitic eggs) were laid on days 9 to 12 of the host's laying period (n = 2), or 1 to 4 days after clutch completion (n = 4). These unmatched eggs may have belonged to floater females that did not subsequently nest, at least in the period immediately following the early season stage.

The proportion of parasitic coot eggs versus host eggs in the same nest that survived a minimum of 15 days was relatively poor (parasitic, $\bar{x}$ = 0.30 ± 0.11; host, $\bar{x}$ = 0.86 ± 0.04; Wilcoxon paired test, Z = 2.51, n = 12 nests, $P < 0.05$; includes one nest with two parasitic eggs from the beginning of the mid-nesting period). Only 28% of these 32 parasitic eggs survived, compared with 90% of 179 host eggs laid during the same period at 18 unparasitized nests. Most of the mortality of parasitic coot eggs resulted from selective host burial (87%, n = 23); an additional 9% of parasitic eggs were found beside the nest cup on the morning after they were laid. Presumably, these eggs were displaced or laid outside the nest during a parasitism attempt. The remaining 4% of parasitic coot eggs disappeared. Of the 12 coot pairs that were parasitized, 67% buried one or more eggs. Mortality of host eggs resulted primarily from their sudden disappearance (78%, n = 18), possibly due to partial nest predation.

To determine factors that triggered the burial response in coots, we augmented our sample of natural parasitic eggs (NPEs) by adding a single experimental parasitic coot egg (EPE) to unparasitized nests on days 4 or 5 of host laying periods. No significant difference occurred in the proportion of EPEs (50%, n = 8) and NPEs (62%, n = 32) that was buried (Fisher exact test, P = 0.41), or in the average number of days that EPEs (4.1 ± 0.66, n = 4) and NPEs (3.9 ± 1.14, n = 7; values for more than one NPE per host were averaged) were left in the nest before they were buried (Mann-Whitney U = 11, P = 0.57). Therefore, we combined data from nests with EPEs and NPEs in the following analyses.

Coot hosts took from one to nine days to bury parasitic eggs that were laid in their nests (median = 3.5, n = 11 nests). Parasitic eggs that looked similar to host eggs were not left in the nest for significantly longer ($\bar{x}$ = 3.8 ± 1.1 days, n = 4) than eggs scored as different ($\bar{x}$ = 3.3 ± 0.56 days, n = 5; Mann-Whitney U = 8, $P > 0.62$; values for parasitic eggs believed to be from the same female were averaged). Hosts also showed individual variation in whether they accepted or buried parasitic eggs. Again, this variation did not seem to be related to how similar or different parasitic eggs were to host eggs, although in the only two cases where coot pairs accepted one parasitic egg and buried another, they accepted an egg that was more similar to their own. Overall, of the 10 coot eggs that were scored as similar to the host's, five were buried and five were accepted. Of the 17 eggs that were scored as different, 10 were buried and 7 were accepted (Fisher exact test, P = 0.71) . In addition, whether a parasitic coot egg was buried or accepted (NPEs and EPEs combined) was not related to whether the egg appeared early or late in the host's laying period (buried, $\bar{x}$ = 5.5 ± 0.79 days after the host's first egg, n = 10; accepted, $\bar{x}$ = 7.9 ± 1.54 days, n = 8; Mann Whitney U = 27, P = 0.24; in nests with more than one parasitic egg, only the first egg was used). If we categorize pairs that buried at least one parasitic egg as rejecters and those that never buried an egg as acceptors, 62% ($n = 16$) of the coot pairs were rejecters and 38% were acceptors.

The nesting period for Lesser Moorhens was much shorter than that of Red-Knobbed Coots, being confined to a three-week period in February (84% of 32 clutches were initiated between 4 and 14 February). Despite surveying the same area intensively in March, no moorhen nests were found. Nest-predation rates were high; 58% of the 33 known moorhen nests were lost to predators. The high predation rate precluded some of the analyses that were done for coots.

Twenty-one percent of 28 complete clutches of moorhens received one or more parasitic eggs. This represented 6% of the 186 eggs laid. If we include one depredated nest in which we found two buried eggs that differed from the shell halves that were found in the nest, the proportion of parasitized nests increases to 24%. However, most of the moorhen nests were found with more than half or all of their clutch complete. If we include any egg in completed clutches that was different in size, shape, and spotting pattern from the host eggs as probable parasitic eggs, then the maximum proportion of parasitized nests increased to 36% (from 6 to 10 nests, $n = 28$), and the proportion of parasitic eggs increased to 11% (from 11 to 21 eggs, $n = 186$). In the following analyses of the patterns of parasitism and host responses, we maximize the small sample sizes by using known plus probable parasitic eggs.

Moorhen hosts received from one to four parasitic eggs ($\bar{x} = 2.1 \pm 0.31$, $n = 10$), with seven of the 10 parasitized hosts receiving two or more eggs. In four of these seven nests, all of the parasitic eggs within the nest matched each other, indicating that the same female probably laid them. The average number of parasitic eggs laid by individual females (assuming a parasitic female laid in only one nest) was 1.6 ± 0.18 (range 1 to 3, $n = 13$).

The timing of laying of parasitic moorhen eggs with respect to host laying periods was known within one to three days for 6 of 10 nests. Four of these six nests received parasitic eggs at least two to eight days after clutch completion, and the remaining two nests were parasitized when hosts were laying the last one-third of the clutch. One additional nest was found early in the nesting period (10 February) with a complete clutch of seven eggs and three probable parasitic eggs that presumably were laid during the host's laying period. Because of high nest predation, we were unable to determine the identity of parasitic moorhens.

No parasitic eggs (from 15 total) survived from eight moorhen nests for which we knew the breeding outcome, compared with 0.32 ± 0.16 survival for host eggs (three of eight clutches totaling 19 of 48 eggs) from the same nests (Wilcoxon paired test, $Z = 1.63$, $P = 0.10$). Mortality of parasitic moorhen eggs resulted from predation (67%), burial (27%), and damage (6%). Four parasitic eggs remained in the nest one to three days before being buried. If we assume that any parasitic egg that remained in the nest for five or more days was accepted and exclude eggs that were in a nest for less than five days before being depredated, then 4 parasitic eggs from two moorhen nests were buried and 10 others from five nests were accepted.

Discussion.—Conspecific brood parasitism was common in Red-knobbed Coots and Lesser Moorhens that bred in ephemeral wetlands in northeastern Namibia. The high rate of CBP in Red-knobbed Coots (43%) was similar to that found in American Coots in western Canada (41%; Lyon 1993a). The average number of parasitic eggs that hosts received and the average number of parasitic females per nest also were similar between the two coot species, but a much larger proportion of parasitic eggs was laid during the hosts' laying periods in Red-knobbed Coots (80%) than in American Coots (55%). In both species, the largest percentage of parasitic eggs was attributed to females that parasitized neighbors before subsequently nesting themselves, with fewer eggs being attributed to females that lost their nests or to possible floater females (i.e. parasitic eggs that did not resemble any others in the area).

Lesser Moorhens had a higher rate of CBP (21 to 36%) than did Common Moorhens in England (8 to 16%; McRae 1995, 1997a). When nest-predation rates were high, the percentage of nests parasitized increased in Common Moorhens (16%; McRae 1997a) but was lower than the most conservative estimate of parasitism in Lesser Moorhens (21%). In other comparisons, hosts of both moorhen species received similar numbers of parasitic eggs, but none survived in Lesser Moorhen nests, primarily because of nest predation and host rejection in the form of egg burial. In Common Moorhens, parasitic eggs also had a lower chance of survival than host eggs, but this was mainly due to parasitic eggs being laid outside host laying periods, when they are unlikely to hatch. However, any parasitic Common Moorhen eggs laid during host laying periods had a higher chance of hatching and a higher probability of survival to independence (McRae 1995).

Parasitizing nests of conspecifics is thought to be either a condition-dependent or mixed breeding strategy. It is a condition-dependent strategy if floater females are unable to secure a nesting site of their own, or if the parasites are young birds or females in poor condition that choose not to nest and thus are "making the best of a bad situation" (Eadie and Fryxell 1992, Lyon 1993a, Sorenson 1993, McRae 1997a). There is no evidence that floater females are specialist parasites (Lyon 1993a). As a mixed breeding strategy, females exhibit opportunistic parasitism before or after commencing laying in their own nest, thus allowing individuals to increase reproductive output without increasing parental effort (Eadie and Fryxell 1992, Jackson 1993, Lyon 1993a, Sorenson 1993, McRae 1997a).

Our results suggest that most Red-knobbed Coots adopt a mixed reproductive strategy by laying parasitic eggs in neighbors' nests before nesting themselves; parasitism by female floaters and females that have had their egg laying interrupted by nest loss seems to be less important. In addition, nesting females laid a larger proportion of their parasitic eggs during host laying periods than did presumed floater females. This pattern of parasitism is almost identical to that found in American Coots (Lyon 1993a, b). We were unable to ascertain which females were parasites in Lesser Moorhens.

One factor that may be promoting high rates of parasitism in both Red-knobbed Coots and Lesser Moorhens is synchronized nesting, which is a consequence of seasonal rains that trigger the arrival of many birds at the breeding grounds. However, nest synchronization alone cannot explain high rates of CBP in Namibia. Whiskered Terns (*Chlidonias hybridus*) and Eared Grebes (*Podiceps nigricollis*) arrived en masse at the same time and shared the same nesting habitat as Red-knobbed Coots and Lesser Moorhens, yet rates of parasitism were much lower for these species (S. McRae and I. Jamieson unpubl. data). Perhaps selection for parasitism in rails is enhanced by other factors such as indeterminate laying and large clutch size, combined with a limit to the number of offspring that a breeding pair can raise successfully (Yom-Tov 1980, Sorenson 1992, Lyon 1993a).

Laying eggs late in the evening or at night also may facilitate parasitism. By checking three coot nests every 3 h after sundown, we determined that eggs were laid sometime after midnight, which is similar to the time of laying found in American Coots and Common Moorhens (Lyon 1993a, McRae 1996). Using video cameras at nests of Common Moorhens, McRae (1996) observed that parasitic females approached a target nest quietly under the cover of darkness and then moved quickly to the nest, pushed aside the incubating bird (normally the male at night), laid an egg, and then departed, all in the matter of a few seconds. Perhaps Red-knobbed Coots and Lesser Moorhens employ a similar tactic.

Rejection of conspecific parasitic eggs based on host recognition and discrimination is rare in birds, and when it does occur, the overall frequency of rejection tends to be low (Arnold 1987, MacWhirter 1989). The two species we studied exhibit a high rate of rejection of parasitic eggs in the form of egg burial. The proportion of parasitic eggs buried by Red-knobbed Coots (67%) was substantially higher than that found in American Coots (33%; Lyon 1993a, b). The high rejection rate in Red-knobbed Coots presumably reflects higher costs of parasitism, which may be associated with a higher proportion of parasitic eggs being laid during host laying periods.

A much more striking difference in host response behavior to parasitic eggs was found between Lesser Moorhens and Common Moorhens. Lesser Moorhens bury parasitic eggs in a fashion similar to that of coots, but only a single case of egg burial has ever been recorded in Common Moorhens (S. McRae unpubl. data). Common Moorhens desert nests in which experimental eggs were added in the early stages of the host's laying period, although natural rates of desertion due to parasitism are low (<1%). Although rates of parasitism appear to be lower in Common Moorhens than in Lesser Moorhens (see above), and the relative costs of parasitism to hosts also appear to be low (Gibbons 1986, McRae 1995), the observation that Common Moorhens desert parasitized nests under certain circumstances suggests that the costs are sufficient to select for nest desertion. If hosts could distinguish their own eggs from those of parasites, egg burial would always be a less costly response than nest desertion followed by renesting. Burying a parasitic egg in the nest presumably is a better response than egg ejection per se because the latter behavior could result in predators being attracted to the nest. Therefore, in light of our discovery of elaborate burying behavior in a congener, why don't Common Moorhens bury parasitic eggs?

The answer to this question presumably relates to annual rates of parasitism, which may be too low in Common Moorhens to evolve effective egg recognition. The associated costs of parasitism may also be low relative to the costs of making a mistake and burying the wrong egg (see Davies et al. 1996). The fact that Common Moorhens in England did not reject Hottentot Teal (*Anas hottentota*) eggs that were dyed bright red and experimentally added to their nests indicates that egg recognition is poorly developed (McRae 1995). However, a recent experimental study of captive Common Moorhens in Belgium, where parasitism rates were high (40% of nests), demonstrated that females had egg-recognition capabilities because they responded differently when an egg from one of the host female's earlier clutches was added to the nest than when another female's egg was added (M. Petrie pers. comm.). Yet, the host female's response to the foreign egg added to her nest always was desertion rather than burial.

That Lesser Moorhens can recognize and reject parasitic eggs is an important finding because it illustrates that well-developed discriminatory powers have evolved in moorhens, and when parasitized, they are capable of using this ability to bury parasitic eggs. These results suggest that egg burial is not part of the behavioral repertoire of Common Moorhens. It may be that high rates of nest parasitism in Common Moorhens are a relatively recent event associated with birds breeding in high densities in parks and other modified habitats, and that egg burial has not yet evolved, although the single observed case of egg burial in McRae's study (see above) would suggest that the strategy exists in the population at a low level.

Finally, the question of why a certain proportion of Red-knobbed Coots and Lesser Moorhens did not bury parasitic eggs but instead accepted and incubated them remains unanswered. Additional research is necessary for a better understanding of the factors related to the evolution of nest parasitism and host responses in both of these species. Unfortunately, the inability to predict years when significant rainfall will trigger mass migration to a breeding site means that carrying out such research will be on an opportunistic basis.

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