When female birds choose already-mated males as their mates, they suffer some costs. One of the major costs is a reduction in male parental care. Feeding by polygynous males decreases in later-hatched broods, or in broods of subsequently mated females (Martin 1974; Patterson et al. 1980; Alatalo et al. 1982; Dyracz 1986; Muldal et al. 1986; Bruun et al. 1997). When nesting cycles of polygynously mated females proceed smoothly, a female that chooses an already-mated male as her mate will be a parent of the later-hatched brood, and will incur the cost of reduced male assistance.

Nest predation is one of the major interruptions of the normal nesting cycle (Ricklefs 1969; Martin 1993) and changes the allocation of male parental care between previously and subsequently mated females (Temrin & Jakobsson 1988; Urano 1990). If a previously mated female fails in her breeding attempt and does not renest within the male’s territory, the subsequently mated female will receive male assistance exclusively. Therefore, the frequency of nest predation influences the probability that subsequently mated females receive male assistance. To evaluate the cost of polygyny in a population, it is important to know both the nest predation rate and the relationship between female mate choice (whether an unpaired male or an already-mated male) and their brood status during the nestling-rearing period.

I studied the effect of nest predation on the allocation of male parental care in the Black-browed Reed Warbler Acrocephalus bistrigiceps. This paper pres-
ents data showing how polygynous males assist in caring offspring. I also report the percentage of females that become mothers of assisted broods when they pair with unpaired or already-mated males. Finally, I discuss the extent of effect of nest predation on the cost of polygyny in this species.

**METHODS**

1) **Study area and species**

This study was conducted during the 1993–1997 breeding seasons in a 42.4-ha area of rice fields along the Arakawa River (36°52′N, 139°35′E; 8 m asl) in central Honshu, Japan. The study area included patches of scattered grassland, which consisted mainly of the common reed *Phragmites communis* and goldenrod *Solidago altissima*. The grassland is the breeding habitat of Black-browed Reed Warblers. The environment of the study area is described in detail in Hamao (2000).

The Black-browed Reed Warbler is a small (ca. 10 g), migrant passerine bird that is endemic to Northeast Asia, and is a summer resident of Japan (OSJ 2000). Males arrive at the study area from late May to mid-July and attract females by singing long, complex songs (Ueda & Yamaoka 1998; Hamao 2000). Females arrive at the site from early June to mid-July, and soon settle in the males’ territories. Females build nests alone, taking widely varying periods to complete the nests (Hamao 2001). The modal clutch size is five. Although a female can produce fledglings twice in a breeding season, it is very rare. During one breeding season, 25% of the males acquired two, or rarely three, females, 56% acquired one female, and 19% remained solitary (Hamao, unpublished data).

2) **Field observations**

Birds were captured in mist nets soon after arrival, and were individually color-ringed. In some cases where females were building nests when I detected them, I marked the females after they laid their third egg to avoid making the females desert their nest. Using this marking method, no bird disappeared from the territory or deserted its nest. The study area was visited daily from late May to mid-August, except in cases of heavy rain. To monitor pair formation and nesting stage, I visited each of the territories daily or every two days, between sunrise (0440±15 min during the study period) and 0800, and observed the behavior of marked birds from a 1.8-m-high stepladder. Observations were made for 15–40 min in each territory. During my visits, I also inspected the nest contents. If all the eggs or nestlings in a nest disappeared, I assumed that it was due to predation.

The nest predation rate was based on observations of all nesting attempts that were identified before egg-laying started. Sixty-five such nesting attempts were identified, including renesting by females within the original territory. Data on mate choice, whether a female formed a pair-bond with an unpaired male or with an already-mated male, were obtained for 49 females. Forty-eight breeding females were observed from the time they settled in their territories, or from the early stage of nest building. I also included in this data set one female (#91) that I found after her clutch was complete. When I found this female, another female (#90) was also nesting within the same territory, and the male was apparently solitary before he paired with female #90. Therefore, female #91 clearly paired with the male who had already mated with female #90.

If a female renested with the same mate after nest predation, I used the final nesting attempt as the result of her mate choice. If the first nesting failed during the incubation period and the next nesting produced fledglings, I assumed that the female had produced eggs that hatched.

3) **Parental activities**

To monitor the incubation and feeding to nestlings by parents, I recorded the birds that visited focal nests with a Sony CCD-G100 video camera and a Sony GV-100 video recorder. The video recording was made for 2.6±0.2 h (mean±SE, N=43). To investigate incubation behavior, I videotaped the nests 5.2±0.7 days (N=13) after the last egg was laid, and to examine feeding behavior, I videotaped the nests 6.0±0.3 days (N=30) after the first egg hatched. The individuals recorded in the videotapes were identified by their leg rings, and I checked to see whether they incubated eggs and fed nestlings.

To describe parental activities, I divided the broods into three categories according to the situation on the day the nests were videotaped. When there was one nest in a territory, the brood was called a monogamous brood. When there were two nesting attempts within a territory, the brood at the more advanced nesting stage was assumed to be the primary brood and the one at the less advanced nesting stage was assumed to be the secondary brood. This definition reduced the number of secondary broods that I could...
videotape, because it was uncommon for both broods of polygynously mated females to survive until the day I made video recordings, due to the high predation rate (see results). The time spent incubating by each parent was measured for nine monogamous, two primary, and two secondary broods. The share of feeding by parents was based on data obtained from 19 monogamous, eight primary, and three secondary broods. The nestling age at the time of video recording did not vary among the three brood categories (monogamous: 5.9±0.3 days (mean±SE), primary: 5.6±0.5, secondary: 7.0±1.2; Kruskal-Wallis test, H=1.36, P=0.51). The number of nestlings in a nest also did not vary among the categories (monogamous: 3.6±0.2, primary: 4.1±0.3, secondary: 4.0±0.6; H=2.57, P=0.28).

To describe relation between mating and hatching order, I divided the broods into three categories by the same way according to the situation on the day the eggs hatched.

4) Statistical analyses
I compared the feeding behavior of different pairs in three brood categories: monogamous, primary, and secondary broods. Since the variance among the categories was unequal, I performed the robust rank-order test (Siegel & Castellan 1988) corrected by the sequential Bonferroni method (Rice 1989). All the statistical tests were two-tailed. Values are presented as means±SE.

RESULTS
1) Male parental care
Males seldom incubated eggs, irrespective of the brood status. Males did not participate in incubating primary or secondary broods. They incubated only three of nine monogamous broods, and the time that they spent incubating (3.6±1.2 min h⁻¹, N=3) was much shorter than that by their mates (31.5±2.0 min h⁻¹, N=3).

The frequency of male food delivery varied between the monogamous, primary, and secondary broods (Fig. 1a). Males never fed the secondary broods. Male feeding frequency differed significantly between monogamous and secondary broods (U=∞, P<0.005). Male feeding frequency also differed between primary and secondary broods, but the difference was not significant (U=5.72, 0.05<P<0.10).

The frequency of female food delivery did not differ significantly between any pairs in the three brood categories (all P>0.2; Fig. 1b). Therefore, the frequency with which both parents fed secondary broods was slightly lower than the frequency with which both parents fed monogamous and primary broods (Fig. 1c), but the differences between any pair of the three brood categories were not significant (all P>0.1).

2) Nest predation
Of 65 breeding attempts, 35 failed because of nest predation. Five of the nests were deserted by both parents. Two of the nests were destroyed when farmers cut the grass supporting the nests. Consequently, 23 nests produced fledgling. Excluding the two cases of artificial destruction, 56% of the nests (N=63) were preyed upon in the study area.

3) Relation between mating and hatching order
Thirty-five females paired with unpaired males,
and 10 (29%) of them disappeared from the territories before egg-hatching, due to nest predation (nine cases) or nest desertion (one case; Fig. 2). Therefore, 25 (71%) of the females that paired with unpaired males produced eggs that hatched. When the eggs hatched, the mates of 15 females remained monogamous (Fig. 2), while the mates of 10 females became polygynous. In the cases of polygyny, nine females were the mothers of primary broods at egg-hatching; i.e. the subsequently mated females were at a less advanced nesting stage (Fig. 2). However, one female became the mother of a secondary brood; i.e. the subsequently mated female was at a more advanced nesting stage (Fig. 2). This inversion in the order of the nesting cycles of the polygynously mated females occurred because the previously mated female built a nest three times before egg-laying, which prolonged her pre-laying period, and by the fact that her clutch was larger than that of the subsequently mated female, which also delayed the start of incubation (Fig. 3a). Therefore, 69% (24/35) of the females that paired with unpaired males became the mothers of monogamous or primary broods at egg-hatching.

By contrast, 14 females paired with already-mated...
males, and five (36%) of them disappeared from the territories before egg-hatching, due to nest predation (Fig. 2). Therefore, nine (64%) of the females that paired with already-mated males produced eggs that hatched. At egg-hatching, five females became the mothers of monogamous broods (Fig. 2), because the previously mated females had disappeared due to nest predation (four cases; Fig. 3b), or because renesting of the subsequently mated female due to predation delayed her egg-hatching, and the previously mated female and her fledglings disappeared in this interval (one case; Fig. 3c). One subsequently mated female became the mother of a primary brood during the nestling-rearing period, because the previously mated female’s nest was preyed upon (Fig. 3a). Three females that paired with already-mated males became the mothers of secondary broods, so their status did not change throughout the nesting period. Therefore, 43% (6/14) of the females that paired with already-mated males became the mothers of monogamous or primary broods at egg-hatching. This proportion (6/14) did not differ significantly from the proportion of females (24/35) that paired with unpaired males ($\chi^2=2.79$, df=1, $P=0.10$).

**DISCUSSION**

Male Black-browed Reed Warblers did not feed later-hatched broods. This can be a potential cost when a female chooses an already-mated male as her mate. In some cases, however, female status changed between the time of pair formation and nestling-rearing. In this discussion, I exclude the status change from a monogamous to a primary brood, which occurs when the mate of a female succeeds in mating polygynously, because it does not affect male parental assistance to the female. With one exception, in which the nesting cycle of a polygynously mated female became inverted (Fig. 3a), any change in female status was caused by nest predation. When a previously mated female failed in her breeding attempt and disappeared from a territory, the subsequently mated female acquired monogamous status (Fig. 3b). This type of status change has been pointed out previously (Temrin & Jakobsson 1988; Urano 1990), Temrin and Jakobsson (1988) reported that almost half of the subsequently mated females of the Wood Warbler *Phylloscopus sibilatrix* had exclusive male assistance because the nests of the previously mated females were preyed upon. I found another type of female status change: renesting of a subsequently mated female due to nest predation delayed her nesting cycle and resulted in her gaining monogamous status at egg-hatching (Fig. 3c).

The proportion of females acquiring monogamous or primary status at egg-hatching was higher for females that paired with unpaired males than it was for females that paired with already-mated males, although the difference was not significant. Therefore, although female Black-browed Reed Warblers will not necessarily receive male parental assistance more readily when they pair with already-mated males, nest predation allowed 43% of the females that chose already-mated males as their mates to receive male assistance. This suggests that nest predation reduces the cost of polygynous mating. If females incur a cost due to time constraints, for example, when they choose males, a female might pair with an already-mated male.

It is worth noting that when more than half of all nests were preyed upon, 69% of the females that paired with unpaired males and 43% of the females that paired with already-mated males acquired the status of the mothers of assisted broods. These proportions indicate the extent of the effect of nest predation on the cost of polygyny in this reed warbler population.

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