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Kin Association in Japanese Quail Chicks

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With 5 figures

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Abstract

Japanese quail (*Coturnix coturnix japonica*) have finely-tuned kin-recognition abilities that may serve a role in mate choice. To investigate whether these abilities are expressed in other life stages, we examined patterns of association among quail chicks in the laboratory four days after hatching. Hatchlings were reared either in mixed-family groups, consisting of siblings and nonsiblings, or in pure-family groups, consisting just of siblings. Chicks were highly social in testing sessions, as reflected in their clumped spatial distributions, and interacted more with their siblings than with nonsiblings. Siblings in each of four mixed-family groups preferentially associated with one another over nonsiblings. No discrimination was evident among differently marked siblings in four pure-family groups. Thus, at an early age, quail discriminate between siblings and nonsiblings despite social experience of both. Recognition abilities that develop prior to or soon after hatching may facilitate cooperation among chicks, may enable siblings to track each others' traits as they mature, or both.

Introduction

The ability to recognize and respond differentially to close genetic relatives facilitates the expression of kin-directed behaviour that may be favoured by kin selection (HAMILTON 1964) or by selection for mate choice (BATESON 1980, 1983; SHIELDS 1983). Many animals recognize their kin, and kin-recognition abilities may influence important aspects of behavioural repertoires (see reviews by GADAGKAR 1985; SHERMAN & HOLMES 1985; HEPPER 1986; FLETCHER & MICHENER 1987; PORTER 1987; WALDMAN 1988). Recognition may be elicited by cues borne by individuals or classes of individuals, but social discrimination is

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expected only in limited social and ecological conditions (WALDMAN 1987). Furthermore, recognition abilities may be influenced by experience during certain life stages but remain latent until they are expressed later in life (e.g., BATESON 1979).

Sexually mature Japanese quail (*Coturnix coturnix japonica*), that have been reared with their siblings, show finely-tuned kin-recognition abilities, approaching novel first cousins more frequently in a testing apparatus than either novel third cousins, siblings, or unrelated individuals (BATESON 1982). Moreover, quail initially reared in sibling groups that subsequently mate with first cousins begin laying fertile eggs on average 3—5 days earlier than those that mate with siblings or more distant relatives (BATESON 1988). These results suggest that quail may choose to mate with close kin, but not siblings, perhaps as a result of selection for "optimal outbreeding" (BATESON 1978, 1980, 1983). Mating preferences of quail are influenced by their social experiences as chicks (BATESON 1978, 1980), and presumably kin-recognition abilities begin to develop early during ontogeny.

In this study, we examine sib-association tendencies of Japanese quail chicks reared in mixed-family groups to ascertain whether they discriminate between siblings and nonsiblings. Because visual characteristics appear sufficient to elicit kin recognition in adults (BATESON 1982) and because plumage changes substantially with maturation, individuals should delay learning these traits until they provide a strong indication of adult appearance (BATESON 1979). Yet chicks might recognize one another by vocal or chemical cues as well as visual cues. Even if they obtain no immediate advantages from discriminating between kin and nonkin, chicks might be expected to keep track of their siblings' traits as they mature, interacting differentially with siblings and nonsiblings throughout development, so that they can learn their siblings' adult plumage characteristics at the appropriate time.

Materials and Methods

Study Animals

Japanese quail (*Coturnix coturnix japonica*) eggs from 12 mated pairs were collected in our laboratory colony. Members of pairs were taken from different stocks, and none of the pairs had common parents or grandparents. Each pair's eggs were placed simultaneously into a separate compartment within a 37.5°-C incubator, where they were held for 13 days and then transferred, again in family groups, to separate compartments within a hatching incubator. Within a few h of hatching (in the dark), chicks were marked with individually numbered tags, and were then assigned to one of 8 groups. Four experimental ("mixed-family") groups were formed with four chicks from each of two families. Four control ("pure-family") groups were each formed with 8 chicks, all siblings from the same brood. Each group consisted of a different family or families, and was housed in a separate pen for four days. Although all groups were visually isolated from one another, chicks could hear vocalizations and smell odours from groups housed in adjacent pens.

Pens were constructed of hardboard, and measured 60 × 44 × 20 cm high. They were illuminated by two 80-W fluorescent lamps on a 16L : 8D photoperiod. Temperature in the pens was maintained at 38 °C by infrared heaters, positioned directly above each pen. Chicks were fed on ground turkey starter crumbs, and had continual access to water from automatic drinkers placed inside the pens.

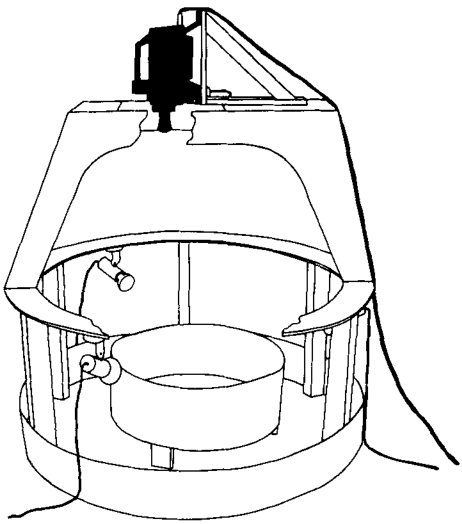

Fig. 1: Testing apparatus for measuring the spatial distribution of quail chicks. Chicks were placed into the inner cylindrical arena, and their movements were recorded by an overhead video camera

Testing Apparatus and Procedure

Four days after hatching, patterns of association among chicks in each group were recorded in a circular testing arena (58 cm diameter). Chicks could move freely over a clear Perspex sheet, but they were confined within the arena by a Perspex cylinder (28 cm height). A grid (7 × 7 cm squares) was placed beneath the Perspex sheet to facilitate later data analysis. The entire apparatus was housed within a chamber constructed of white hardboard. Chicks' movements were recorded by a Hitachi colour camera (GP-6 MK; zoom lens) positioned at the top of the chamber, 90 cm above the chamber floor (Fig. 1). Video recordings were made with a Hitachi portable video cassette recorder (VT-6500). The chamber was illuminated and heated by four overhead 100-W incandescent lamps. Temperature was regulated at 38 °C by a thermostatically controlled exhaust fan. Chicks inside the apparatus could not see outside the chamber, and appeared to acclimate quickly once placed into the testing arena. Neither food nor water were available in the testing apparatus.

Prior to each test, chicks in test groups were marked on their dorsal feathers with small adhesive paper circles labelled in black ink with either a cross or a circle. For control groups, these markings were randomly assigned; for experimental groups, members of each sibship were marked differently. The pure or mixed-family group was then placed into the testing arena, and chicks were allowed an initial 30-min acclimation period. Their movements were then video-recorded for 30 min. The group was then returned to its pen, the base and sides of the apparatus cleaned, and another group tested similarly.

Data Analysis and Statistics

Video recordings of each group's movements were played back with a Panasonic NV-8500 recorder on a 39-cm diagonal monitor. Recordings were viewed continuously and, at 60-s intervals, each individual's position and marking was recorded on a gridded data sheet. To preserve independence between replicate measures, data from a recording period were discarded if any individual did not move during the previous 60-s interval.

The data were digitized on an Apple graphics tablet (model A2M0029) interfaced with an Apple II computer. Two-dimensional Cartesian coordinates were obtained for each individual by arbitrarily setting the centre of the arena to be the origin point. Coordinates were transformed into unit values based on the radius of the testing arena. These data were uploaded to an IBM 3081 mainframe for further analyses.

For every recording period, linear distances were computed between each of the 8 chicks. In experimental tests, distances were determined between each individual and its nearest sibling and nonsibling. Mean sibling and nonsibling nearest-neighbour distances were then computed for each recording period. In addition, mean-neighbour distances to siblings and nonsiblings were computed for each recording period based on the distances of every individual to each of its siblings and nonsiblings, excluding the distance of each individual to itself. In control tests, the same computations were made, comparing distances between each individual and its siblings labelled with either the same or different marking.

If chicks moved randomly in the testing arena, they ordinarily would be expected to be closer to nonsibling than to sibling nearest neighbours (in control tests, to dissimilarly rather than to similarly marked siblings). This null expectation occurs because each individual can interact with three other individuals belonging to its own group, but with four individuals belonging to the other group. Nearest-neighbour data were thus corrected to account for this discrepancy. Based on random positional data (repeatedly generated using NAG subroutine RNUNI, Numerical Algorithms Group), expected values of sib — nonsib and sib — sib nearest-neighbour distances were determined; actual data were transformed into proportions of the appropriate expected values. The result was a ratio of observed over expected nearest-neighbour distances. Nearest-neighbour ratios greater than 1.0 thus suggest regular (uniform) distributions, while those less than 1.0 suggest contagious (clumped) distributions (see SOUTHWOOD 1978). Mean-neighbour distances were not similarly standardized because expected values did not differ significantly (also see discussion in WALDMAN 1986a).

For experimental tests, sib and nonsib nearest-neighbour ratios and mean-neighbour distances were compared by repeated-measures analyses of variance. The same analyses were conducted for control tests, comparing ratios and distances between similarly and dissimilarly marked siblings. Each analysis constitutes a 2 × 2 factorial design of less than full rank because data were omitted during recording periods when individuals had not moved (on average, 2 records per 30-min interval). Sums of squares were estimated by univariate models (General Linear Models procedure of SAS version 82.4, using Type III estimates; see FREUND & LITTELL 1981).

Results

In each of the experimental tests, chicks preferentially associated with their siblings. Nearest-neighbour ratios were less than 1.0 for all tests, indicating that chicks showed clumped distributions with both siblings and nonsiblings (Fig. 2). However, nearest-neighbour ratios were significantly less between siblings ($\bar{x}$ = 0.70) than between nonsiblings ($\bar{x}$ = 0.78) ($F_{(1, 3)} = 10.28$, $p < 0.05$). Similar

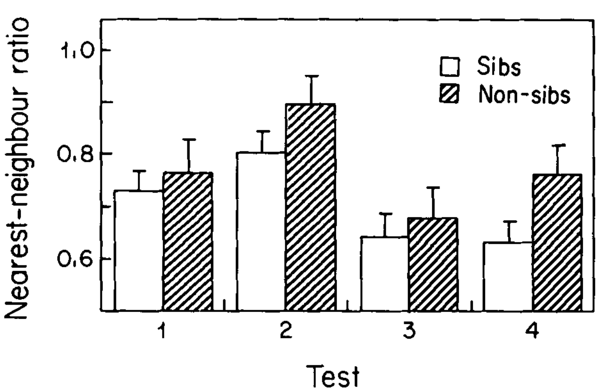

Fig. 2: Mean distances between nearest-neighbour siblings and nonsiblings in each of four experimental tests. Measurements are expressed as ratios of actual distances observed over those expected if chicks moved randomly in the testing arena. Nearest-neighbour ratios less than 1.0: clumped distributions; above 1.0: regular distributions; Bars: SE

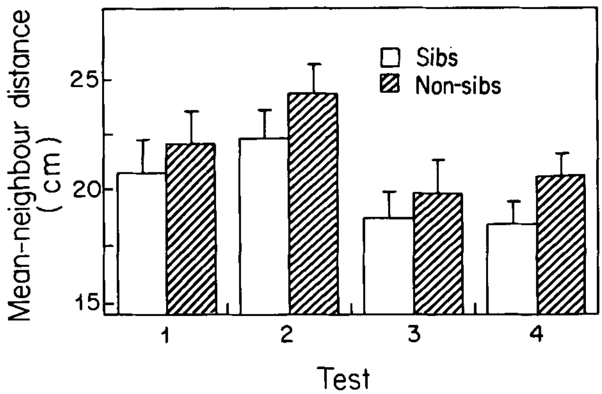

Fig. 3: Mean distances between all siblings and nonsiblings in each of four experimental tests. Bars: SE

effects are apparent in analyses of mean distances. In each test, chicks were on average closer to siblings ($\bar{x}$ = 20.3 cm) than to nonsiblings ($\bar{x}$ = 22.0 cm) (Fig. 3), and this difference was highly significant ($F_{(1, 3)} = 40.52$, $p < 0.01$).

Control tests failed to reveal differences when groups consisted entirely of siblings. Clumping patterns of siblings were similar to those tested in mixed groups (Fig. 4). But nearest-neighbour ratios between similarly marked individuals ($\bar{x}$ = 0.68) and dissimilarly marked individuals ($\bar{x}$ = 0.69) did not differ

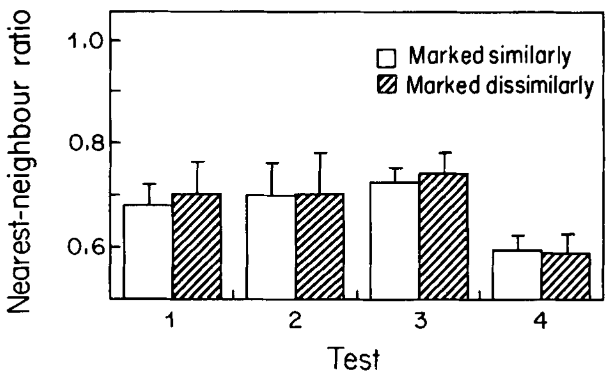

Fig. 4: Mean distances between nearest-neighbour individuals in each of four control tests. All individuals are siblings, but they are differentially marked to ascertain the effect of marking procedures. Measurements are expressed as ratios of actual distances observed over those expected if chicks moved randomly, as in Fig. 2. Bars: SE

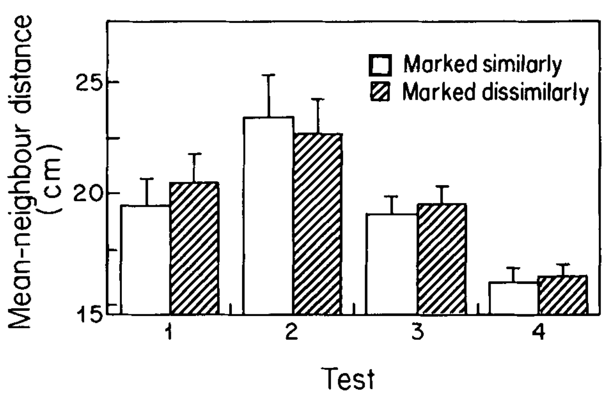

Fig. 5: Mean distances between all individuals bearing the same mark and between those bearing different marks in each of four control tests. Bars: SE

significantly ($F_{(1, 3)}$ = 1.22, p = 0.35). Mean distances among similarly marked individuals ($\bar{x}$ = 18.6 cm) did not differ from those among dissimilarly marked individuals ($\bar{x}$ = 18.8 cm) ($F_{(1, 3)}$ = 0.68, p = 0.47) (Fig. 5).

Discussion

Quail chicks recognize their siblings, by four days after hatching. And they discriminate behaviourally between siblings and nonsiblings even though they have had social experience of both. While we cannot eliminate experience prior to or during the few hours after hatching as a determinant of kin preferences in these experiments (see TSCHANZ 1968; GOTTLIEB 1971), hatchlings in the incubator had no visual cues available to them, and these cues elicit kin-discrimination responses in adults (BATESON 1982). Sibling groups were placed into separate compartments within the incubator, but chicks could smell and hear both their siblings and nonsiblings. Respiratory clicks produced by quail embryos prior to hatching may serve as a cue by which individuals synchronize their hatching (VINCE 1966; VINCE et al. 1984), but these sounds are nonspecific and are unlikely to be important in later social interactions.

When chicks became mobile, in the rearing pens, individuals were able to freely interact with both their siblings and nonsiblings. As precocial birds, quail apparently develop the ability to recognize kin prior to or immediately after hatching. Their ability to distinguish between familiar siblings and familiar nonsiblings suggests that either individuals or sibling groups have distinct labels, and that labels of interacting conspecifics do not converge. Quail chicks may have recognized conspecifics whose labels were similar to their own, or possibly, they individually recognized those siblings with which they were housed in the incubator. Alternatively, chicks may have associated with their siblings because of differential, possibly genetically influenced preferences for local features of the environment (see discussion in WALDMAN 1982). The laboratory testing arena, however, was relatively featureless.

Neither the labels that identify kinship nor the developmental processes by which the labels are perceived are revealed by this study. SALZEN & CORNELL (1968) found that domestic chicks that had been artificially coloured and socially isolated subsequently tended to associate with individuals that were the same colour as themselves (also see VIDAL 1982). Recognition thus may be assessed by the comparison of morphological labels. Other phenotypic labels, including odours, vocalizations, and even behavioural characteristics, might also be effectively compared. In mixed groups, for example, chicks might tend to associate with individuals that behave in the same manner as themselves. Individuals are likely to synchronize their locomotor behaviour with others whose activity rhythms resemble their own.

The social preferences of Japanese quail chicks are influenced by the learning process known as "imprinting" (RUBEL 1970). Quail chicks exposed to a stuffed female develop a preference for that model over another female (SCOTT 1981). Our present results suggest, however, that before imprinting has substantially influenced their social preferences, another developmental mechanism may come into play, inducing the chicks to respond preferentially to their own kin. This does not mean that this mechanism and imprinting normally operate in opposition to each other. On the contrary one might guide the other so that, when surrounded by kin and nonkin, chicks selectively attend to and become especially familiar with kin.

That learning reflects selective responsiveness of individuals to species-specific cues has been demonstrated in studies of song acquisition (reviewed in KONISHI 1985) and filial imprinting (e.g., GOTTLIEB 1971). But selectivity may extend even further and enable individuals to develop specific kin-recognition abilities if, due to some form of stimulus-filtering, traits of close relatives appear particularly salient (WALDMAN 1986b). Thus, the selective responsiveness of birds that are about to imprint (see BATESON 1987) is more subtle than previously supposed.

Whether similar processes may influence the development of kin-recognition abilities in other birds is unknown. Bank swallow (*Riparia riparia*) chicks recognize their siblings if they hear their calls, and this preference appears to be acquired in the nest because chicks hear their nestmates vocalize. Chicks can thus be induced to recognize a familiar but unrelated conspecific (BEECHER & BEECHER 1983). Canadian goose (*Branta canadensis*) chicks discriminate between familiar (possibly siblings) and unfamiliar conspecifics as early as 3 days after hatching, but social preferences increase over the first 15 days, probably due to experience (RADESÄTER 1976). Rooks (*Corvus frugilegus*) appear to recognize individuals with which they were reared as nestlings, regardless of whether they are genetically related (RØSKAFT & ESPMARK 1984). Studies on other birds also suggest that sibling recognition results in large part from learning (e.g., GOTTLIEB 1968, 1971; EVANS 1970; ZAJONC et al. 1975).

Our measures of sibling association, nearest-neighbour and mean-neighbour distances, reveal small but consistent tendencies for siblings to be closer to one another that to nonsiblings. The magnitude of these differences, from 8 to 11 %, is comparable to those typically found in measures of kin discrimination (e.g., O'HARA & BLAUSTEIN 1981; WALDMAN 1981; HOLMES & SHERMAN 1982). Clumping patterns of siblings in the experimental tests were similar to those shown by siblings in the control tests. While nonsiblings also tended to clump in the experimental tests, they maintained larger distances among themselves than did siblings. In these experiments, at least, siblings appeared to be more attracted to one another than were nonsiblings. This is not the only mechanism by which sibling associations might form. In some amphibian larvae, for example, siblings form clumped distributions but nonsiblings move randomly or actively avoid one another (see review in WALDMAN 1986a). In quail chicks, by contrast, kin associations appear to be superimposed on a general tendency of all familiar conspecifics to interact socially.

Little is known about the natural history or behaviour of Japanese quail in the wild, so the functional interpretation of these results is difficult. Should chicks share food resources or otherwise cooperate in a manner that augments their inclusive fitness, tendencies to associate with siblings might be selected early in development. Later in life, the possibility of close inbreeding may be reduced by differential dispersal patterns. But even if it is not, individuals that can recognize their siblings may avoid mating with those individuals (BATESON 1980, 1982). Aside from providing inclusive-fitness benefits during early ontogeny, preferential kin association during this period may serve to familiarize individuals with their siblings' traits as they mature. Although the mechanisms by which quail recognize their close kin require further study, our findings raise the possibility that kin discrimination may provide multiple, perhaps interrelated, functional benefits.

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