

A Social Relations Model for the Colonial Behavior of the Zebra Finch

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A social relations model was developed for 5 years of behavioral recordings from a captive colony of Zebra finches (*Taeniopygia guttata*). A quantitative ethogram was applied, using one-zero focal animal sampling on an ethologically comprehensive checklist of 52 behavioral items (Figueredo, Petrinovich, & Ross, 1992). Of the 9 ethological factors previously identified, only 4 of the 6 social factors (Social Proximity, Social Contact, Social Submission, and Social Aggression) were used. Major results were as follows: (1) Individual finches showed systematically different response dispositions that were stable over a 5-year period as both subjects and objects of behavior; (2) Interactions between finches differed systematically by the sexes of both the subjects and the objects of behavior; (3) Behavioral interactions between finches and their mates differed systematically according to the subjects' sex, but also differed systematically from those with other members of the objects' sex; (4) Behavioral interactions between finches and their relatives differed systematically between different discrete categories of relatives, but did not vary as a systematic function of either graded genetic relatedness or familiarity due to common rearing; and (5) Behavioral interactions between finches and their relatives showed an overall bias towards preferential interactions with male relatives.

Keywords: Social Relations Modeling, Zebra Finch, Ethological Factor Modeling, Longitudinal, Multiple-P-Type Factor Analysis

This paper presents a social relations model based on five years of behavioral recordings from a captive colony of Zebra finches (*Taeniopygia guttata*) (Passeriformes: Estrildidae). This species of Australian desert grassfinch has been called the "white mouse" of birds because of its many desirable properties as an avian model for: (a) social development; (b) sexual development; (c) vocal development; and (d) substratal neuroanatomy, neurophysiology and behavioral endocrinology (for classic reviews of the various separate bodies of research literature on the Zebra finch (see Burley, 1986; DeVoogd, 1986; Slater, Eales, & Clayton, 1988; Konishi, Emlen, Ricklefs, & Wingfield, 1989; ten Cate, 1989). The present study provides a quantitative ethological framework on which to base a program of integration between all these diverse aspects of Zebra finch psychobiology.

Figueredo et al. (1992) previously applied confirmatory factor analysis to identify and provide construct validation for the latent ethological *states* characterizing species-typical patterns in Zebra finch behavior; Figueredo, Cox, and Rhine (1995) previously applied generalizability analysis to document the internal consistency and interrater reliability of the latent personality *traits* characterizing individual differences in Zebra finch behavior. The present social relations model is an attempt to integrate those findings within a single quantitative framework.

The Social Relations Model

The Social Relations Model (SRM) was first described by Kenny and La Voie (1984) and focuses on the study of dyadic relationships. This method is different from others in that it selectively partitions variance attributable to the relationship from those attributable to

individual response dispositions. In SRM there are three main components: actor effects, partner effects, and relationship effects. *Actor effects* refer to the behavior of individuals when averaged across all of their interactions with all other individuals in the sample. *Partner effects* refer to the average behavior elicited by an individual across all dyadic interactions. *Relationship effects* refer to the specific behavioral tactics a given individual uses when interacting with another specific individual. While SRMs are typically used to understand human populations, they can also be used for the study of animal interaction, as is done in the present study.

There are many SRM designs (Kenny & La Voie, 1984). In *Checkerboard* designs, there are fewer dyadic interactions and they form a patchwork “checkerboard” pattern across the matrix of possible interactions; in *Circle* designs, each participant interacts with one partner such that each participant is connected to one another in a circle form; in *Block* designs, individuals are split into two groups and the members of one group interact with members of the other group but not with members of their own group. In *asymmetric* Block designs, there is a distinguishable prior difference between the groups (e.g., males versus females), whereas in *symmetric* Block designs, there is no systematic difference between groups because participants are randomly assigned to the two groups. The most popular design, however, is *Round Robin*, which was the one used in this study. In the Round Robin design, every participant is free to interact with every other participant in the sample.

SRMs have four major assumptions: (1) interactions are exclusively dyadic, meaning that there are no extradyadic interactions such as an actor with multiple partners; (2) participants are randomly selected from the population; (3) there are no order effects in the interactions, and (4) actor, partner, and relationship effects are additive and the relationships are linear (Kenny & La Voie, 1984). SRMs can handle both random and fixed effects.

SRMs have been used in many research areas. They have been used for describing relationships in friendship groups (Kenny & Kashy, 1994), and describe dyadic relationships between clients and therapists in group therapy (Marcus & Kashy, 1995). For example, Kenny and Kashy (1994) used an SRM to describe interpersonal perception of personality in friendship and acquaintance groups. In particular, they investigated the effects of *co-orientation*, where friends have the same view of the world. These effects are 1) *consensus*, the extent to which individuals agree in their ratings of a single person, 2) *assimilation*, the extent to which one views others as similar to themselves, 3) *self-other agreement*, the extent to which one's perception of oneself agrees with others' perception of them, and 4) *assumed similarity*, the extent to which one thinks others are similar to themselves. To establish who was considered a friend and who was considered an acquaintance subjects were asked to rate who they liked the most and those who picked each other were classified as friends. This introduced special dyadic relationships into the model, so to compensate, the researchers used a specialized version of the round robin called a Dyad Round Robin to analyze the results. This study was of same-sex friends (symmetric) and the designation of dyad membership (*i.e.*, A or B) was arbitrarily selected. They found that consensus, assimilation, and assumed similarity were higher in the friendship group compared with the acquaintance group.

The Round Robin design is particularly popular for studies set in a speed-dating event. Finkel and Eastwick (2008) discuss speed dating events coupled with social relations model analysis as a way to better understand romantic relationships and relationship attraction. Speed dating designs for heterosexual individuals group participants according to their sex (in an asymmetric Block design) and rotate participants so that each person gets to meet every other person of the opposite sex. Usually there are an equal

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number of males and females, but when the number of males and females is unequal, the extra participants sit out for some interactions, but eventually rotate through the entire group.

Persons and Situations

Chamove, Eysenck and Harlow (1972) utilized psychometric methodology and relatively complex statistical analyses of social interaction data to document stable personality traits in nonhuman primates. Data were obtained from observations of social behaviors, such as social exploration, social play, and hostile contact. Factor analyses of these behaviors revealed three strong, almost independent factors, *hostile*, *fearful*, and *affiliative/sociable*, noting that these factors are very similar to the *psychoticism*, *emotionality*, and *extraversion* factors often found in humans. The researchers concluded that "This observational study demonstrates marked individual differences between monkeys in their social behavior. These differences are apparently highly reliable, and characteristic of the animals concerned, and may thus be regarded as aspects of the 'personality' (p. 502-503)." Houts, Cook, and Shadish (1986) used an SRM-like model to identify *person effects* (similar to the actor effects of Kenny and La Voie 1984), *situation effects*, and *person-by-situation interaction effects* in humans. As shown by theorists like Epstein (1979, 1980, 1983), the relative strength of these numbers probably resided in the degree of data aggregation possible with this kind of data.

Figueredo, Jacobs, and colleagues have used classes of adaptive problems to organize a principled taxonomy of environmental contexts (Figueredo et al., 2007; Figueredo et al., 2010a; Figueredo et al., 2010b). Any *environmental context* can be partitioned into abiotic *settings* and biotic *situations*. Biotic situations can then be partitioned into *interspecific* and *intraspecific* situations. Intraspecific situations can be partitioned into *extrafamilial* and *intrafamilial* situations, including *parent-offspring* situations and *sibling-sibling* situations. Both extrafamilial and intrafamilial situations can be further partitioned into *intrasexual* and *intersexual* situations. Intrasexual situations include *male-male* and *female-female* cooperation and competition. Intersexual situations include *male-female* and *female-male* cooperation and competition. In the present paper, we apply social relations models to partition behavioral interactions among Zebra finches according to this taxonomy, distinguishing intrafamilial from extrafamilial situations, intrasexual from intersexual situations, and cooperative from competitive situations.

The underlying principle behind this taxonomy is that these different types of contexts present different adaptive problems to the organism. For example, abiotic settings present different adaptive problems from biotic situations. Nonliving material does not respond with counterstrategies to the adaptive behavioral tactics of an organism. If a polar bear evolves white fur for better camouflage, the ice does not change color to thwart the bear. In contrast, if a polar bear evolves a certain new behavioral tactic for catching arctic seals, the selective pressure generated by this new behavior promotes the evolution of corresponding antipredator tactics by the prey to avoid capture by any predator using the new tactic. Similarly, conspecifics pose different adaptive problems than allospecifics. Competition, for example, is generally higher among conspecifics because they require and consume similar resources, which may be limited in any given environment. The theory of kin-selected altruism predicts that social interactions will be markedly different among genetic relatives than among nonrelatives in that more cooperation is expected to evolve among relatives. The theory of sexual selection predicts that social interactions will be markedly different among members of the same sex than among members of the opposite sex in that more competition is likely to evolve among members of the same sex in obtaining and retaining mates of the opposite sex. This principled taxonomy of

contexts therefore partitions the environment according to the nature of the adaptive problems presented, rather than in an arbitrary fashion. Broadly speaking, this taxonomy should be applicable to both human and nonhuman animals. In the present study, we apply this taxonomy to the colonial behavior of the Zebra finch.

The Natural History of the Zebra Finch

The estrildid finches are small passerine birds of the Old World tropics and Australasia. The estrildid finches of the Australian continent evolved with its aridification, which transformed greater Australia from widespread rain forest to a cover of grassland (Zann, 1996). Zebra finches are extremely well adapted to arid grasslands with erratic rainfall. Their adaptations include their ability to travel long distances in search of water, breed non-seasonally, obtain water from sources not available to other estrildidines, and physiology that allows for water extraction from food sources, in addition to very low water requirements. Zebra finches evolved in an unpredictable, dry environment. Despite their remarkable adaptation to their environment, limiting factors for Zebra finches include water availability, rainfall (for the production of grass seed for food), and high rates of predation. The Zebra finch's diet consists almost entirely of grass seed. An average clutch size of five chicks requires constant foraging and feeding by both parents. The Zebra finches' ability to breed without regard for season allows them to take advantage of unpredictable rainfall and the ripening grass seed that these conditions bring. If conditions permit (*i.e.*, adequate amounts of food are available), Zebra finches are capable of several months of continuous breeding. Breeding has been documented in all months of the year in several areas and in several cases for 12 months or longer in a row. The spatial and temporal predictability of food and water is low because both are dependent on rainfall, which is unpredictable across Australia.

Zebra finches are a colonial species that, during the breeding season, live in groups ranging from 5 to 25 breeding pairs, with a group of unpaired individuals and young birds living in close vicinity of the breeding pairs. All individuals congregate several times daily for social meetings where they feed, sit, bathe, and preen one another (Immelmann, 1965, 1969; Zann, 1996). Zann (1996) observed that colonies range in size from 24-229 adults per colony during breeding cycles and between 20-350 adults per colony during periods of non-breeding. Population sizes can vary widely. During periods of sustained drought population sizes have plummeted. Surviving Zebra finches congregate in large numbers around reliable water sources during especially dry periods. Relatively wet years result in population growth. During these years large numbers of small breeding colonies are formed, which exist across Australia with the exception of the rainforest.

Until recently Zebra finches were thought to be nomadic; colonies seemed to travel from region to region in search of adequate breeding conditions. Immelmann (1965) observed large-scale nomadism to the outskirts of Zebra finch territories in years of severe drought, and he assumed that in non-drought years colonies would also travel in a nomadic fashion, on a smaller scale, until they found adequate conditions for breeding within the interior of the species' boundaries. Extensive observation by Zann (1996) revealed that nomadism is a mischaracterization of their behavior. Except in years of severe drought, smaller Zebra finch colonies exist as subgroups of larger populations centralized around a reliable water source. Small bands or colonies periodically break away from this "home base" to breed. Larger "home base" colonies are composed of differing categories of individuals. These categories include: (1) breeding adults that may periodically leave for breeding excursions to a breeding site within flying distance of a reliable water supply, (2) pre-fledgling juveniles, (3) new adults that become

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part of the breeding population and (4) immigrants that may stay to become part of the colony or just stop to rest and travel through to the colony they will eventually live with. Large "home base" colonies therefore have a fluid membership that smaller breeding colonies break off of for breeding and rejoin when not breeding.

The Present Study

Few published SRM studies rely purely on observations of spontaneous interactions between freely associating individuals. The Zebra finch represents an ideal species for aviary study because of adaptation to social living. The advantages of this animal model include its colonial nesting habits, non-seasonal (opportunistic) breeding, and non-territorial courtship song. In addition, its natural habitat is similar to the general semi-arid climate of Arizona, the environment in which the present study was conducted and in which the colony thrived. Although the captive colony used could not possibly simulate all the conditions of its natural habitat, it served as a naturalistic and relatively unconstrained setting for spontaneous social interactions.

The main hypotheses of this study are as follows: (1) there will be statistically significant main effects of both subjects (social actors) and objects (social partners) of behavior, indicating systematic individual response dispositions as both social actors and social partners; (2) there will be statistically significant interactions between particular subjects and objects of behavior, indicating dyadic interindividual social relationships that deviate from a simple additive model of individual response dispositions; (3) there will be statistically significant main effects of both subject sex and object sex; (4) there will be statistically significant interactions of subject sex with object sex; (5) there will be statistically significant main effects of specific interindividual social relationships, such as between the mated members of sexual pair-bonds, among clutches of siblings reared together, among specific categories of relatives (*e.g.*, brothers, half-brothers, cousins, uncles, *etc.*), and according to the continuous coefficient of relatedness (proportion of shared genes) between any two individuals.

Method

Participants

The participants were adult members of a healthy and vigorous captive colony of Zebra finches. An original stock of 14 breeding adults was introduced in June of 1988. The first 43 offspring produced (all those fledged in 1988) remained and matured in the parental colony, yielding a maximal population of 57 resident adults. After that time, the monthly removal of new juveniles became necessary to keep the study population manageable for detailed behavioral observation. The subject population therefore varied systematically through time and is described in more detail under the sampling procedures. All the consanguineal (genetic) and conjugal (sexual) relationships among colony members were systematically tracked over the years by means of the Family Tree Maker program.

Apparatus

A walk-in aviary was constructed 7.25 km northwest of Tucson, Arizona. This aviary measured 3 x 3 x 2.5 m and was provided with an inner 1 x 1 x 2.5 m double-door antechamber.

The top was roofed over at an angle, guttered and rainproof, but the 1.25 cm galvanized wire mesh sides were otherwise open to the elements. The interior was provided with multiple wooden nest boxes, placed about 0.6 m apart, and several multi-tiered wooden perches (with multiple crossbars at staggered right angles) hanging at different heights, each about 1.2 m tall and 1 m in diameter. A 2 x 2 x 9 m double-door entrance was located at the northeast corner to prevent any birds from escaping. Twelve 10x10x10 cm wooden nest boxes were evenly spaced 1.5 m up from the floor up to the ceiling on the east wall. The density of the birds in the aviary did not exceed that of more densely populated breeding colonies found in the wild (Zann, 1996).

The Zebra finches were free fed Arizona Feeds brand finch mix birdseed manufactured by Eagle Milling, 4743 N. Highway Dr., Tucson, AZ, with one ounce of Clovite brand horse vitamins manufactured by Fort Dodge Animal House, Fort Dodge, Iowa, stirred in for every pound of seed. They were also provided with water, grit, and cuttlebones. Dried timothy grass and 2 cm diameter cotton rope was cut into 2-3 cm lengths, shredded and used for nesting material. The method used by Mann and Slater (1994), *i.e.* repeated behavioral observations of nest building and maintenance, was used to assign residency in nest boxes and parentage of chicks. Residency in nest boxes was established when an individual was observed moving nesting material into a nest box on repeated occasions. The Size C numbered metallic and colored plastic bands used to identify individual birds were purchased from A.C. Hughes, Ltd., Middlesex, United Kingdom. The colors used were selected to have neither positive nor negative effects upon Zebra finch sexual attractiveness to conspecifics (N. Burley, personal communication).

Electronic "clickers" were constructed to pulse regularly every 30 seconds. These were connected to commercially available amplified speaker units to time the onset and offset of each observation interval. The birds did not appear to respond in any way to the sound of the clickers, perhaps due to habituation. Data were recorded on standardized checklists.

Procedure

The basic behavioral sampling system used was an adaptation of one developed for use with cercopithecine monkeys, validated over 18 years of continuous use with a captive colony of macaques at the University of California, Riverside, as well as upon wild troops of baboons in a field site at Mikumi, Tanzania (Figueredo et al., 1992). The system is a form of One-Zero Focal Animal Sampling, which is useful for the simultaneous sampling of multiple behaviors on a single individual (the "focal animal") at a time. Because one or more occurrences of any specific behavior within a sampling interval are scored as a 1, and none as a 0, making no distinction between single and multiple occurrences of that behavior within sampling intervals, the observer is freed, for the remainder of that interval, to concentrate on recording other behaviors. One-Zero Sampling has been shown, both with primate data and through Monte Carlo simulations, to have extremely high multiple correlations with the weighted sum of behavioral frequencies and durations (Rhine & Flanigan, 1978; Rhine & Linville, 1980; Rhine & Ender, 1983), typically exceeding .95 with sampling intervals as long as 120 seconds, thus providing a single composite index of both frequencies and durations of interaction.

One-Zero Focal Animal Sampling (at 30-second intervals) was used to collect data on color-banded individuals using an ethologically comprehensive checklist (the quantitative ethogram) of 52 specific behavioral items. Birds were sampled randomly (with replacement) as focal animals for observation. Focal animals were followed continuously during observation sessions of 5 minutes each. In this sample, although it was not possible to sample every subject every day, all colony adults were available to be sampled as focal animals. All 57 adults in the colony were selected randomly as focal animals, or *Subjects* of behavior; 61 individual birds were recorded as

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non-focal animals, or *Objects* of behavior, because of the interactions observed between the adults and several additional juveniles. The total number of dyadic interactions observed during the entire five-year period among these individuals was 2620.

Data Encoding and Aggregation

The 30-second interval one-zero "hits" (i.e., sampling intervals with scores of 1) were summed across each series of consecutive intervals (each totaling 5 minutes), for each separate behavioral item, yielding numerical item scores. Each one-zero "hit" was identified by the code for the identity of the individual actor, or *Subject* of the behavior, and that of the social partner, or *Object* of the behavior. Raw item scores were averaged across two independent observers, theoretically producing a mean score that is more reliable than either score reported separately by either of the two observers. Each observer was required to complete a six-week training period to an interobserver reliability criterion of 0.90. To monitor the stabilities of the interobserver reliabilities after the initial training periods, all observations used in this study were taken simultaneously by two independent observers and the reliability computed for every data collection season. The final reliabilities of all data used in the social relations model are reported below.

Common Factors. Common factor scores are generally more reliable and valid than single indicator scores. Results of social relations models previously applied in primatology often unstable across alternative behavioral items, even when they are parallel indicators of same construct (see Rhine & Ender, 1983; Rhine & Flanigan, 1978; Rhine & Linville, 1980). Common factor scores increase the stability of the solution in social relations models.

Figueredo et al. (1992) originally identified nine common factors in the quantitative ethology of the Zebra finch: three Affiliative factors, (F1) Singing and Parenting, (F2) Social Proximity, and (F3) Social Contact; three Agonistic factors, (F4) Social Submission, (F5) Social Aggression, and (F6) Sex and Violence; and three Individual factors, (F7) Object Handling, (F8) Surface Foraging, and (F9) General Activity. Of these nine factors, only two Affiliative factors, (F2) Social Proximity and (F3) Social Contact, and two Agonistic factors, (F4) Social Submission and (F5) Social Aggression, were used in the present SRM. A complete listing of the items indicating each of these common factors can be found in Figueredo et al. (1992).

The Affiliative factors were organized by the *magnitude* of the acts, indicating "strong" versus "weak" interactions between individuals, and not by the *direction* of the acts; the Agonistic factors were instead organized by the *direction* of the acts, e.g., "done by" versus "done to" any particular individual, and not by the *magnitude* of the acts.

Social Proximity (F2) and Social Contact (F3) are primarily distinguished by spatial congregation, such as mutual "approaching" and "remaining near", versus actually physically touching, and such as mutual "allopreening" and "contacting", which suggests increasing degrees of closeness in an affiliative relationship. In addition, whereas "undirected singing" is negatively correlated to Social Proximity (F2), "being sung to" is positively correlated with Social Contact (F3), which suggests very different social contexts for what appear to be the same vocalizations, modulated only by "directedness" as a metacommunicative signal.

Social Submission (F4) and Social Aggression (F5) are primarily distinguished by the direction of the agonistic act, such as "squawking", "threatening", and "charging", which suggest degrees of relative dominance in an agonistic relationship. "Fleeing without pursuit" correlates with Social Submission (F4), however, indicating that this factor is not merely defined by the passive receipt of aggressive behavior but is characterized by an active avoidance response (and one apparently accepted by the aggressor, who does not offer pursuit). Similarly, the more

perseverating agonistic behaviors, such as "chasing", "beak fencing", "tail pulling", and "feather plucking" are significantly correlated with Social Aggression (F5), but not reflexively with Social Submission (F4).

Because the multivariate groundwork has been adequately laid, it was not necessary to perform needless repetitions of the complex modeling procedures detailed by Figueredo et al. (1992); the present data were analyzed by computing validated and meaningful factor scores based on the psychometric results of the previous study. "Unit weighted" factor scores (Gorsuch, 1983), in this case simple unweighted averages of raw scores because all the indicators are expressed in a common metric, were estimated by aggregating across all the significant indicators of each common factor.

Categories of Subjects, Objects, and Relationships. Individuals within a colony can be grouped into categories, such as sex or age group, which may account for some fraction of the behavior. For example, males generally tend to be more aggressive than females. Additionally, the existence of specific relationships between individuals can also be used to help predict their behavior. The relationship between a Zebra finch mother and her offspring is generally more affiliative, for example, than a relationship between unrelated individuals. We can therefore use the knowledge of these types of relationships to help predict and account for other types of behavior.

Thus, in addition to *Subjects* and *Objects* and their interactions, several categories were constructed for classes of individuals and interindividual social relations. *Subject Sex* was the sex of focal animal, or individual actor; *Object Sex* was the sex of target of behavior, or social partner; *Mate* was the sexual pair-bond partner of any given individual; *Clutch* designated a group of siblings reared together; *Kin* denoted the coefficient of relatedness (proportion of shared genes) between any two individuals, expressed as a continuous variable; and *Categorical Code* denoted a specific groups of relatives (*e.g.*, brothers, half-brothers, cousins, uncles, *etc.*)

Interactions between these categorical variables represent any special relationships that may exist between entire categories of individuals or of relationships (*e.g.*, males may allopreen females more than females allopreen males).

Statistical Analyses

Statistical analyses were performed using the SAS 9.1 software package. Analyses of variance were performed using the SAS ANOVA and GLM procedures; univariate means and bivariate covariance matrices were obtained using the SAS MEANS and CORR procedures.

A Social Relations Model (SRM) is a specific type of hierarchical General Linear Model (GLM) in which every individual (the *Subject* of a behavior) is related to every other individual (the *Object* of a behavior) in a colony (or group of individuals) with respect to some type of behavior. An SRM is like a repeated measures ANOVA design in that for every subject there is not one observation, but several observations. Table 1 displays a representative illustration of a social relations matrix.

In a social relations matrix of aggressive behavior, for example, the mean number of each individual's aggressive interactions with every other individual in the colony is calculated. The number that relates a specific pair of individuals is the mean number of aggressive interactions for that pair, and a matrix composed of cells relating every individual with every other individual is thereby created. The birds, that are the subjects of the behaviors, are represented by the columns and the birds that are the objects of behaviors are represented by the rows in the matrix. The cells of a matrix are made up of the average of all of the observations of the interactions between two birds.

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Table 1
Schematic Representation of the Social Relations Model

<i>Subjects</i>	<i>Objects</i>							
	Males			Females				
	1	2	3	4	5	6		
Males	1	C ₁₁	C ₁₂	C ₁₃	C ₁₄	C ₁₅	C ₁₆	\bar{x}_{1*}
	2	C ₂₁	C ₂₂	C ₂₃	C ₂₄	C ₂₅	C ₂₆	\bar{x}_{2*}
	3	C ₃₁	C ₃₂	C ₃₃	C ₃₄	C ₃₅	C ₃₆	\bar{x}_{3*}
Females	4	C ₄₁	C ₄₂	C ₄₃	C ₄₄	C ₄₅	C ₄₆	\bar{x}_{4*}
	5	C ₅₁	C ₅₂	C ₅₃	C ₅₄	C ₅₅	C ₅₆	\bar{x}_{5*}
	6	C ₆₁	C ₆₂	C ₆₃	C ₆₄	C ₆₅	C ₆₆	\bar{x}_{6*}
		\bar{x}_{*1}	\bar{x}_{*2}	\bar{x}_{*3}	\bar{x}_{*4}	\bar{x}_{*5}	\bar{x}_{*6}	

Note. c_{ij} = Cell Mean; \bar{x}_{i*} = Row Mean; \bar{x}_{*j} = Column Mean.

A single observation, or *occasion* of measurement, was comprised of the time and date the observation was made, the identification of the subject of the behavior, the identification of the object of the behavior and the common factor of which that behavior was a representative. Every cell within a social relations matrix represents the mean of the scores of the observations taken on the two birds specified by the cell. The type of behavior entered into the cell (*e.g.* aggressive, submissive, and affiliative) is specified by the type of social relations matrix. There were four social relations matrices in this study, one for each of the four social common factors analyzed.

The cell means (c_{ij}) of the social relations matrix for each common factor were calculated by averaging all of the scores for the behaviors that were indicators for that common factor. For example, c_{34} is the cell mean that, over several sampling occasions, defines the aggressive relationship of Bird 4 directed toward Bird 3. There are two cells for every pair of individuals on each behavioral matrix. For example, in one of two of these cells, Bird 3 is the subject of the behavior and Bird 4 is the object. Observations including "Bird 3 chases Bird 4" would be recorded in this cell. "Bird 4 chased Bird 3", however, would be recorded in the reciprocal cell, *i.e.* c_{43} . If all of the observations of Bird 3 with every other bird were averaged, therefore taking the column mean for Bird 3, the average score for his aggression would be obtained. The score for a subject's aggressiveness, averaged across all object birds, is used as an overall measure of aggressiveness. If however, a particular bird has a level of aggressiveness that is not relatively high, but has a very high cell mean for aggressive behavior with only one particular bird, those two birds have an especially aggressive relationship. These two birds therefore have an aggressive relationship that is not explained by the organizing principles that define either bird. Therefore a social relations matrix works to define the nature of the relationships between the individuals within a colony.

In summary, within the social relations matrix, *Subject Effects* are indicated by row means representing the degree to which each individual generally behaves (*e.g.*, aggressively) with respect to all other individuals within the colony; *Object Effects* are indicated by column means representing the degree to which each individual is generally the target of others' behavior (*e.g.*, is aggressed on) averaged across all other individuals within the colony; and *Subject*Object Interaction Effects* are indicated by cell means indicating special relationships between any two individuals when significantly different from that predicted by the row and column means (*e.g.*, an especially aggressive or submissive relationship). Row and column means represent main

effects of individuals (*Subject, Object*); Cell means represent interactions between two particular individuals (*Subject*Object*); Nested effects represent categories of individuals or of relationships (*Subject Sex, Object Sex, Mate, Clutch, Kin, Categorical Code*); and interactions between groups represent relationships between entire categories of individuals (*e.g., Subject Sex*Object Sex*). Thus, within an SRM, multiple measurement *occasions* are nested within social *situations*, which represent a broader category of occasions that can be tested as systematic effects.

Results

Interrater Reliabilities

All observations used in this study were taken simultaneously by two independent observers and the reliability computed for every season in which social relations data were collected. A complete tabulation of interrater reliabilities by sampling season is provided in Table 2. These are expressed as intraclass correlation coefficients (unsquared etas).

Table 2
Interrater Reliabilities by Seasonal Samples

Season	Social proximity	Social contact	Social submission	Social aggression
Fall 1988	0.961	0.958	0.856	0.880
Spring 1989	0.980	0.866	0.900	0.964
Fall 1989	0.959	0.917	0.843	0.825
Fall 1990	0.877	0.990	0.866	0.806
Spring 1991	0.894	0.883	0.794	0.866
Fall 1991	0.995	0.959	0.872	0.964
Spring 1992	0.990	0.958	0.913	*
Fall 1992	0.971	0.989	0.964	0.985
Spring 1993	0.890	0.729	0.736	0.910

Note: * Not Observed During Spring 1992.

These interrater reliabilities were all acceptably high. Spring of 1992 is lacking from this sample because the laterality (right/left) of the 52 specific behaviors were recorded for that season instead of the objects of the behaviors. That subsample is therefore not included in the present analyses.

Subject and Object Effects

The main effects of Subjects and/or Objects of behavior were statistically significant for all four common factors. These effects indicate the presence of systematic individual differences in response dispositions as both subjects and objects of behavior.

Social Proximity. Object effects were statistically significant ($F(58,2353)=2.53, p=.0001$). This indicates that certain individuals were attracting other colony members to their immediate vicinity more frequently than others. For example, certain birds were approached more frequently by other individuals than were other birds.

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Social Contact. Both Subject effects ($F(55,2353)=1.41$, $p=.0268$) and Object effects ($F(58,2353)=1.74$, $p=.0005$) were statistically significant. This indicates that certain individuals initiated physical contact with others more frequently than other colony members, and that certain individuals were targeted by other members of the colony more frequently for physical contact as well. For example, certain birds contacted some individuals more frequently than others and certain birds were contacted more frequently by other individuals than were other birds.

Social Submission. Object effects were statistically significant ($F(58,2353)=1.35$, $p=.0429$). This indicates that certain individuals received submissive social signals more frequently than other members of the colony. For example, other birds fled more frequently without pursuit from certain individuals than they did from others.

Social Aggression. Object effects were statistically significant ($F(58,2353)=2.22$, $p=.0001$). This indicates that certain individuals received aggressive social signals more frequently than other members of the colony. For example, certain birds were chased more frequently by other individuals than were other birds.

The remaining predictors test hypotheses regarding the specific categories of individuals (organized by sex, mateship, and kinship class, as well as various combinations of these categories) that were more frequently observed as either subjects or objects of these social behaviors.

Subject Sex and Object Sex Effects

The effects of Subject Sex and/or Object Sex, as either main effects or interactions, were significant in all four common factors. These effects indicate that Zebra finches treated each other differently, not only as individuals, but as members of their respective sexual categories, and that the social exchanges among the sexes were often asymmetrical.

Social Proximity. The main effects of Object Sex ($F(1,2353)=11.84$, $p=.0006$) and the interaction of Subject Sex with Object Sex ($F(1,2353)=24.04$, $p=.0001$) were statistically significant. Males had significantly higher frequencies as objects of Social Proximity behaviors than were females. However, when the subjects were female, males had significantly higher frequencies as objects of Social Proximity behaviors; when the subjects were male, females had significantly higher frequencies as objects of Social Proximity behaviors. For example, males were approached more frequently by females than were females and females were approached more frequently by males than were males.

Social Contact. The interactions of Subject Sex with Object Sex ($F(1,2353)=15.21$, $p=.0001$) and of Subject Sex with Object ($F(53,2353)=2.17$, $p=.0001$) were statistically significant. When the subjects were female, males had significantly higher frequencies as objects of Social Contact behaviors than were females; however, when the subjects were male, females had significantly higher frequencies as objects of Social Contact behaviors than were males. For example, males were contacted more frequently by females than were females and females were contacted more frequently by males than were males.

Social Submission. The main effect of Object Sex ($F(1,2353)=9.33$, $p=.0023$) was statistically significant. Males had significantly higher frequencies as objects of Social Submission behaviors than were females. For example, birds of both sexes fled more frequently without pursuit from males than they did from females.

Social Aggression. The main effect of Subject Sex ($F(1,2353)=16.13$, $p=.0001$) and interaction of Subject Sex with Object Sex ($F(1,2353)=8.96$, $p=.0028$) were statistically significant. Males had significantly higher frequencies as subjects of Social Aggression behaviors

than were females. For example, males chased other birds of both sexes more frequently than did females. However, males had significantly higher frequencies as subjects of Social Aggression behaviors than were females when the objects were female and females had significantly higher frequencies as subjects of Social Aggression behaviors than were males when the objects were male. For example, males were chased more frequently by females than were females and females were chased more frequently by males than were males.

Mateship Effects

The main effects of mateship (statistically controlled for both subject and object sex) were statistically significant in three out of the four factors. This indicates that pair-bonded members of a mated pair, unsurprisingly, treat each other differently than they do other members of the opposite sex.

Social Proximity. The main effect of Mate ($F(1,2353)=323.50$, $p=.0001$) was statistically significant. Pair-bonded birds performed Social Proximity behaviors more frequently with their mates than with other individuals.

Social Contact. The main effect of Mate ($F(1,2353)=352.47$, $p=.0001$) and the interaction of Subject Sex with Mate ($F(1,2353)=39.44$, $p=.0001$) were statistically significant. Pair-bonded birds performed Social Contact behaviors more frequently with their mates than with other individuals. However, this difference was greater for male subjects than for female subjects. For example, pair-bonded males contacted their female mates more frequently than pair-bonded females contacted their male mates.

Social Aggression. The main effect of Mate ($F(1,2353)=8.34$, $p=.0039$) was statistically significant. Pair-bonded birds performed Social Aggression behaviors more frequently with their mates than with other individuals. For example, pair-bonded birds chased their mates more frequently than they did other individuals.

Kinship and Familiarity Effects

Three alternative hierarchical orders of entry for these predictors were used to test several alternative hypotheses for kin recognition (as evidenced by differential social behavior) regarding the role of familiarity versus genetic relatedness:

Hypothesis 1. Familiarity between clutchmates determines social relationships, as in certain primates. The predicted order for Model 1 was therefore Clutch, then Kin, then Categorical Code.

Hypothesis 2. Graded degree of genetic relatedness determines social relationships, as in certain social wasps. The predicted order for Model 2 was therefore Kin, then Clutch, then Categorical Code.

Hypothesis 3. Discrete categories of genetic relatives determine the social relationships, as in certain ground squirrels. The predicted order for Model 3 was Kin, then Categorical Code, then Clutch. Kin had to be tested before Categorical Code to insure that the discrete categories were not significant due to the presumably underlying continuous variable.

Kin (the continuous coefficient of relationship) was not statistically significant in any order tested. Categorical Codes (for specific kinship categories) were generally significant even if entered after Kin. Clutch was not significant if entered after Categorical Code, whereas Categorical Code was generally significant even if entered after Clutch. Model 3 was therefore accepted as the most parsimonious yet explanatory of the three alternative models and the statistical results of that model are reported in this paper. This means that Zebra finches show

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no evidence of detecting a graded coefficient of relationship in their social interactions, but apparently do not distinguish clutchmates from siblings in general as evidenced in their behavior. However, Zebra finches do apparently treat different discrete classes of relative differently for reasons yet to be determined.

Social Contact. There was a significant main effect of Categorical Code ($F(19,2353)=6.33$, $p=.0001$). The rank ordering of frequencies of Social Contact behaviors among categories of kinship were, from highest to lowest, with mothers, then with sons, then with uncles, then with cousins, then with all others. There was also a significant interaction of Subject Sex with Categorical Code ($F(14,2353)=2.62$, $p=.0009$). The rank ordering of frequencies of Social Contact behaviors among categories of kinship for female subjects were, from highest to lowest, with sons, then with uncles, then with cousins, then with half-brothers, then with all others. For example, females contacted their sons more frequently than they did all other individuals. The rank ordering of frequencies Social Contact behaviors among categories of kinship for male subjects were, from highest to lowest, with mothers and then with all others. For example, males contacted their mothers more frequently than they did all other individuals.

Social Aggression. The interaction of Subject Sex with Categorical Code ($F(14,2353)=1.73$, $p=.0447$) was statistically significant. The rank ordering of frequencies of Social Aggression behaviors among categories of kinship for female subjects were, from highest to lowest, with fathers, then with aunts, then with half-brothers, then with uncles, then with all others. For example, females chased their fathers more frequently than they did any other individuals. The rank ordering of frequencies of Social Aggression behaviors among categories of kinship for male subjects were, from highest to lowest, with mothers, then with brothers, then with half-sisters, then with cousins, then with all others. For example, males chased their mothers more frequently than they did any other individuals.

Discussion

Zebra finches show systematic individual differences in response dispositions that are stable over a five-year period both as subjects and objects of behavior. Behavioral interactions between Zebra finches differ systematically by the sexes of both the subjects and the objects of behavior, as well as by an interaction of the sex of the subjects with the sex of the objects of behavior. Behavioral interactions between Zebra finches and their mates differ systematically according to the subjects' sex, but also differ systematically from those with other members of the objects' sex. Behavioral interactions between Zebra finches and their relatives differ systematically between different discrete categories of relatives, but did not vary as a systematic function of either graded genetic relatedness or familiarity due to common rearing. Behavioral interactions between Zebra finches and their relatives appear to show an overall bias towards preferential interactions with male relatives, possibly as an adaptation to the general pattern of female-biased dispersal observed in birds (Clarke, Saether, & Roskaft, 1997).

This partial disjunction between graded and categorical relatedness is reminiscent of the differences between the kinship systems of human matrilineal and patrilineal societies described by social anthropologists, which also deviate from quantitative expectations based exclusively on genetic coefficients of relationship (Reynolds, 1984). Briefly, humans in matrilineal societies tend to interact more with matrilineal kin than with patrilineal kin having equivalent genetic coefficients of relatedness; humans in patrilineal societies tend to interact more with patrilineal kin than with matrilineal kin having equivalent genetic coefficients of relatedness. It has sometimes been argued that the corresponding coefficients of genetic relationship for the same categories of patrilineal kin are somewhat eroded by paternity uncertainty (in relation to the

relative lack of doubts regarding the maternity of human offspring), but the reported rates of misassigned paternity in humans (e.g., Brédart & French, 1999) are generally insufficient to account for the magnitude of the asymmetries observed by social anthropologists on differential affiliation with matrilineal and patrilineal kin in matrilineal as opposed to patrilineal societies. We believe that the same principle holds for Zebra finches: the range of reported rates of misassigned paternity is similar to that of humans for many species of birds (e.g., Charmantier & Réale, 2005). We therefore surmise that social interactions in Zebra finches are probably biased towards male relatives because of the pattern of female-biased dispersal that these birds share with most human societies (e.g., Figueredo et al., 2001), meaning that females are the ones that eventually leave the natal group. Thus, applying the same principled taxonomy of environmental contexts to both human and nonhuman animals may reveal interesting parallels.

Another finding of interest is that, generally speaking, both affiliative and agonistic behaviors had higher frequencies between sexes than within sexes, especially among the members of a mated pair. Similarly, both affiliative and agonistic behaviors had higher frequencies among genetic relatives than among nonrelatives. These intensified levels of social interaction were especially high for mother-son and father-daughter relationships. Closer relationships generally made for higher levels of both social affiliation and social aggression.

In addition, this study also constitutes an empirical demonstration of the scientific utility of the principled taxonomy of situations proposed by Figueredo, Jacobs, and colleagues (Figueredo et al., 2007; Figueredo et al., 2010a; Figueredo et al., 2010b) in the description of social behavior. Furthermore, this SRM integrates the findings of Figueredo et al. (1992) regarding the latent ethological *states* that characterize species-typical patterns in Zebra finch behavior with those of Figueredo et al. (1995) regarding the latent personality *traits* that characterize systematic individual differences in Zebra finch behavior within a single quantitative framework.

Finally, we may also conclude, on a more general methodological note, that SRMs using ethological common factor scores show great promise for the modeling of spontaneous social interactions in Zebra finches, providing much more information about the structure of Zebra finch colonial behavior than simpler methods have been able to reveal. SRMs of ethological data might indeed hold the key to a detailed understanding of the social facilitation of vocal development in birds.

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