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**A transactional analysis of changes in parent and chick behaviour prior
to separation of Herring Gulls (*Larus Argentatus*): A three-term
contingency model**

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Abstract

The effect of the passage of time on parent-offspring behaviour of urban Herring Gulls (*Larus Argentatus*) was studied and analysed using a three-term contingency model. A behavioural sequence was initiated by the arrival of a parental adult gull, which would lead to feeding in the chick. However, with the passage of time, and approach of the separation period, this pattern changed. Chicks' begging became more intense, and parent gulls more often withheld food. However, the chicks' begging became directed at a wider range of adults over the observation period. These activities are placed within a three-term contingency model, which may have implications for understanding some behavioural processes involved in parent-offspring separation.

Key words: Parent-offspring conflict, feeding behaviour, begging signals, approach/avoidance, three-term contingency, Herring Gull.

1. Introduction

The ethological study of gull behaviour has played a significant role in the history of behavioural psychology. Watson (1908) started his career making such observations. Ethology has also impacted both on theoretical accounts of operant behaviour (e.g., Baum & Aparicio, 1999; Crawford, 1986; Timberlake, 1993), and on extrapolations from nonhuman to human behaviour in the applied domain (e.g., Tinbergen & Tinbergen, 1972). However, there have been relatively few attempts to apply the methods of analysis and interpretation developed by behaviour analysis to the issues important to ethologists (but see Timberlake, 1993). It should be noted that an approach involving the integration of associative learning principles and ethology has been attempted for a number of behaviour systems, such as sexual behaviours (Domjan, 1994), and social learning (Domjan, Cusato, & Villarreal, 2000; Griffin & Galef, 2005). More generally, the behaviour systems framework proposed by Timberlake (1993; 1994) is a theoretical approach integrating associative learning with ethological approach to the structure and function of behaviour.

The present report represents a study of parent-chick interactions in the Herring Gull (*Larus Argentatus*) over a period preceding parent-offspring separation and dispersal of the chicks. This period has particular importance for ethology, and for understanding parent-offspring conflict (see Morales & Velando, 2013; Trivers, 1974). Behaviour analytic approaches were used to document these behaviours, and to construct a three-term contingency model of their relationship to one another. The three-term contingency model requires one to identify the antecedent stimuli for a behaviour, the behaviour, and the maintaining consequences of that behaviour (Skinner, 1969). In doing so, it was

hoped to identify some proximate (i.e. immediate) causes of separation and dispersal in light of the behavioural contingencies experienced by the birds in their social setting.

This is especially important given recent suggestions that the behaviour of con-specifics should be treated as important aspects of the environmental control of social behaviours (Domjan et al., 2000). Of course, one such important social setting is parent-offspring interactions.

Chick dispersal affects behavioural systems at multiple levels, including processes important to population ecology, meta-population dynamics, speciation, biogeography, and gene flow (see Clobert, Baguette, Benton, Bullock, & Ducatez, 2012; Jensen, 2001; Korpimäki, Salo, & Valkama, 2011). However, the causes of this important phenomenon are generally not well known, and in the absence of identifiable causes, dispersal is attributed to 'behavioural maturation' of the offspring (see Clobert et al., 2012; Kenward, Marcstroem, & Karlbom, 1993, for overviews). In fact, much of the debate concerning the dispersal of chicks has focused on parent-offspring behaviour. Many articles have addressed this from the perspective of ultimate causes (see Clobert et al., 2012; Trivers, 1974). The change in parent-offspring behaviour is usually attributed to selfish-gene arguments involving appeal to the increased likelihood of reproductive success brought about by movement to more genetically heterogeneous areas (see Asaduzzaman & Wild, 2012; Jensen, 2001). Where proximate or immediate causes have been sought, they have focused on such stimuli as reduced feeding by parents (Baaloudj et al., 2012; Edwards, 1985), and parental aggression (Alonso, Gonzalez, Heredia, & Gonzalez, 1987). This change in focus from genetic/maturation to triggering environmental cues moves the 'releasing' stimuli for behaviour from inside the organism to the outside environment.

However, it otherwise does little to place such stimuli within the contingency framework used often by behaviour analysts.

Domjan *et al.* (2000) presented a model which focuses on the learned aspects of such social situations, and places emphasis on the behaviour of con-specifics as promoting the observed social responses. However, this model presents an account of the possible Pavlovian contingencies at play in social situations rather than using an operant approach. In fact, since the original debates on the relative importance of innate and learned behaviours (cf. Baerends, 1985; Hailman, 1969; Tinbergen & Perdeck, 1950), there has been little work conducted on this topic from an operant perspective. There appear to be two sources for this paucity of work conducted on a range of important behavioural phenomena. One potential reason is the lack of a strong behaviour analytic response to attacks from the 'constraints on conditioning' (e.g., Seligman, & Hager, 1972), and 'species specific' or 'niche learning' (e.g., Plotkin, 2002) hypotheses. Although there have been some refutations of this approach from an operant perspective (see Pellon & Blackman, 1987, for one example of an experimental defence of a general learning approach), most refutations of the 'constraints on learning' literature (e.g., Seligman & Hager, 1972) that suggest the existence of particular tendencies to form some association faster than others (e.g., taste-aversion) have been provided within an associationist framework (Mackintosh, 1983).

More importantly, however, it has proved very difficult to conduct controlled observations that attempt to identify functional relationships between the behaviour of family members during a pre-separation or pre-dispersal period. As noted above, there have been a number of studies concerned with changes in both parent and offspring

behaviour during this period (e.g., Alonso *et al.*, 1987; Baaloudj *et al.*, 2012; Cloberty *et al.*, 2012; Edwards, 1985; Graves, Whiten, & Henzi, 1991; Hailman, 1969; Pugesek, 1990). These studies have noted increases in chick begging (Graves *et al.*, 1991), decreases in parental feeding (Edwards, 1985; Morales & Velando, 2013; Pugesek, 1990), and increases in parental aggression (Alonso *et al.*, 1987; Dickinson & McGowan, 2005). However, few reports have documented the potential relationships of these behaviours to one another (although see Davis & Quinn, 1997). Consequently, little is known about the role of con-specific behaviours in parent-offspring interactions during a period immediately prior to dispersal. If recent suggestions about the importance of studying con-specific behaviours in understanding social interactions are to be investigated, this functionality needs to be examined more closely.

Given the above, the present study was conducted for three reasons. Firstly, to show that a controlled observational study, at the level of the individual, and interpreted within a three-term model, is an appropriate methodology for this area. Secondly, to show that behaviour analytic techniques can construct a potential testable model of parent-chick behaviour prior to separation and dispersal that includes con-specific behaviour as part of its explanation. Thirdly, to investigate whether the changes in parent-offspring behaviour previously noted over a period immediately before dispersal are related to one another.

2. Method

2.1 Subjects

The adult Herring Gull (*Larus Argentatus*) is about 600mm long from the tip of its bill to the tip of its tail. The adult is white and grey/black, and individuals are discriminable from one another. Immature birds are a mottled brown, and are similarly discriminable from one another. Herring Gulls nest in a variety of sites, but always near a body of water. In places where food from human activities is abundant, they nest on buildings. Two or three eggs are laid in mid-May, and are normally incubated for 26–28 days, hatching in mid-June. Typically, one chick a year is successfully reared. These chicks leave the nest at between 40–60 days of age (see Pierotti & Annett, 2001; Pierotti & Good, 1994, for further details of the natural history of these gulls).

In this study, an opportunity sample of three Herring Gull chicks, one chick from each of three nests, and their families were studied. Each of the chicks was fed by two adult gulls. The chicks were approximately 40 to 45 days old at the start of the observation period. The observation was conducted during the period from late July to early August, 2002

2.2 Location

The gulls were observed on their urban nest sites, which, during the period of observation, contained only one chick. The nests were located in various positions on a flat roof, situated on top of a three-story building. Observation was conducted from approximately 20 feet away and from above, from a building on the street opposite the

nest site. The urban setting was located in the southwest of England (Ilfracombe, Devon, on the Bristol Channel). This urban setting had a large colony of urban gulls, some nesting close to the building chosen for a nest site by the subjects of the present study, but no other gulls nested on the site selected for observation. During the period of observation, the weather was hot (between 18-27°C) with one evening downpour. Sunrise occurred at approximately 04:40, and sunset at approximately 20:05.

2.3 Procedure

Observation of the gulls was conducted for two one-hour periods on each of seven consecutive days. The observations were made between 10.30 and 11.30 in the morning, and 16.00 and 17.00 in the evening, approximately. During these observation periods, the behaviour of the chicks and gulls was sampled on an event sampling schedule. Every instance of the behaviour that was observed during the target period was recorded. All three chick-parent sets were observed during each session.

A number of distinct and easily observable behaviours were sampled for recording during the observation. For the adult bird, four separate behaviours were recorded.

2.3.1 Approach/Arrival, which included any adult flying over the nest site, or alighting close to the nest site. If the adult bird alighted close to the nest site, this behaviour was often accompanied by a 'trumpeting call'. This behaviour comprised the adult drawing itself up, and emitting a long series of calls (often thought in gulls to allow chick identification of the parent, *inter alia*, see Charrier, Mathevon, Jouventin, & Aubin, 2001).

2.3.2 Readiness to feed: this refers to the adult standing still on the approach of a chick. The chick when approaching a newly arrived adult gull would almost always emit a series of high pitched 'peeps', while holding their body low and head up. In response the adult would stand still, and place its bill in a position reachable by the chick.

2.3.3 Avoidance: on the chick's approaching and 'peeping', the adult gull would move away from the chick. This was achieved by the adult turning its back to the chick, raising its bill, and quickly moving some distance from the chick. If the chick continue to pursue the adult until the adult could not move away, the adult would continue to hold its bill away from the chick.

2.3.4 Feeding: the adult would present (regurgitate) food for the chick.

Three distinct activities of the chicks were recorded.

2.4.5 Avoidance: the chick moves away from an adult bird. This involved running, often low to the ground, to some area of cover on the roof at a distance from the adult.

2.3.6 Approach: in which the chick would move quickly toward an adult bird, almost always emitting a series of high pitched 'peeps', while holding its body low and head up.

2.3.7 Begging: chicks peck at the red spot on the parent's bill (see Tinbergen & Perdeck, 1950).

The occurrences of these activities were recorded at any point at which they occurred during the observation period. The reliability of these observations was checked by a second observer, who independently made the observations during 10mins of each period. Agreement between the observers was always over 95%.

3. Results

The frequency of the activities of the three gull chicks and adults over the fourteen observation periods (two periods in each of seven consecutive days) was recorded. Although these behaviours were recorded at any point during the observation period at which they occurred, with the exception of adult approach, they never occurred out of a specific sequence and occurred with complete consistency during the observation periods reported. This sequence began with an adult approach to the nest, followed by either a chick approach or avoidance of that adult. This was followed by the adult readiness or avoidance response. If the readiness response occurred, this was followed by chick begging and, usually, subsequent feeding. This behavioural sequence is characterized in Figure 4. Such a sequence was easily discernable, there being no breaks of longer than a few seconds between one activity and the next. Most often, the continuity between successive behaviours was immediate. However, the important point for the initial purposes, is that there were no instances of these behaviours at times other than when the entire behavioural sequence was initiated.

Figure 1 about here

The reactions of the three chicks to the presence of adult gulls in the vicinity are displayed in Figure 1. The number of responses made to an approaching adult parent, and to another adult, for each chick, during each observation period, was calculated. As this number varied between chicks, and between observation periods, the numbers of

chick behaviours in each category was turned into a percentage of the total number of opportunities for that behaviour to be presented; that is, the proportion of times that the chick emitted that behaviour in the presence of the adult when it approached (e.g., if the chick always approached the parent this would be 100% parental approach, if the chick avoided a non-parental adult on 50% of the occasions that a non-parental adult approached, this would be 50%, etc.). These data show that at the start of the observation period, the most common chick response to the arrival of an adult parent was approach to that parent, very often accompanied by the chick 'peeping call'. The chicks' responses to other adult gulls initially could be characterized as avoidance. However, over the course of the observation period, the frequency of the chicks' approach to the parent adult first increased slightly (although it was already at a high rate) and then waned. In contrast, over the course of the observations, chick approach increased in the presence of other adult gulls, and avoidance of non-parental adults diminished.

Figures 2 and 3 about here

Figure 2 shows parental adults' responses to chicks' approach or 'peeping' behaviour expressed as a percentage of the total number of times that the chick approached during an observation period. The number of times that the chicks' approach and 'peeping' resulted in the adult 'readiness response' was initially very high. However, this adult response to chick approach declined over the period of observation. The opposite occurred for the adults avoiding the chick.

The parental adults' responses to the chicks' begging behaviour (bill pecking) following the adults' initial 'readiness response' is displayed in Figure 3. Each activity is expressed as a percentage of all activities engaged upon after the chick's response. At the start of this observation period, about 70% of chick begging responses resulted in the presentation of food to the chick. However, this proportion fell markedly by the end of the period. At the same time as feeding was declining, the adult tended to avoid the chick after the chick's begging increased. There were no observations of parental adult aggression (pecking) directed at the chicks during the period.

The order in which the various activities mentioned above changed also showed relatively consistent trends across the subjects. The level of begging in the chicks from the parent gull increased on Sessions 7, 7, and 3 for Chicks 1 to 3, respectively. Next, the parents began to avoid the chicks more (Sessions 9, 7, and 6 for Adults 1 to 3, respectively). The chicks then began to beg from other adults (Sessions 7, 7, and 10 for Chicks 1 to 3, respectively).

4. Discussion

The purpose of the present series of observations was to document reliable trends in parent-chick interactions over a period preceding separation and dispersal of the chicks. On the bases of these observations, a three-term contingency model of how these behaviours modify over time was constructed. The present observations established a reliable pattern of parent-offspring behaviour, which had a high degree of inter-observer reliability.

At the start of the observation period, the parents of the chicks responded positively to the chicks' requests for feeding. However, this positive response to begging waned over the course of the observation period. Such a change in parental behaviour has been noted previously. Observations made at the time when parental investment in chicks is declining have demonstrated that the parents become less responsive to begging (Graves *et al.*, 1991). Similarly, the amount of time parents withhold food from their offspring following a begging response has been shown to increase as the offspring become older (Pugesek, 1990).

Additionally, the present study noted that the chicks began to beg more intensively over the course of the observation period, and begged from a wider range of adults. A marked increase in begging has been noted in offspring prior to chick dispersal (see Graves *et al.*, 1991), but there are few, if any, documented examples of a greater range of adults being begged from in the literature. The demonstration that chicks' behaviour to particular stimuli connected with feeding (e.g., the parent's red bill spot) changes over time is not novel. For example, Hailman (1969) demonstrated that the bill pecking observed by Tinbergen and Perdeck (1950) does not emerge spontaneously, but has to come under stimulus control to promote feeding and attachment. However, the present observations suggest this process is subsequently reversed before separation and dispersal of the chicks.

Some limitations need to be mentioned concerning the generalization of these results. The current observations were conducted on a limited number of individuals, and greater numbers of subjects would help to secure these behavioural descriptions. Typically, many more individuals are studied in ethological studies, if not in behaviour

analytic studies. However, ethological reports typically do not tend to analyze the data functionally at the level of the individual, as was required for the present purposes. That the observations were detailed at this level of analysis made study of large numbers of individuals difficult. The between-subject reliability achieved in the present study possibly makes the addition of further subjects irrelevant. A second issue limiting the degree of generality to be attached to these data concerns the fact that the gulls studied in the present report were urban dwelling birds. The behaviour of such gulls may be different from those nesting in non-urban environments. However, it should be noted that few (none to the author's knowledge) have demonstrated differentiated behaviour along this dimension between urban and non-urban individual Herring Gulls.

Figure 4 about here

The current observations allow a three-term contingency model of the gull's behaviour to be constructed (see Figure 4); an aspect of behaviour analytic theorizing so far missing from ethological studies. This model uses the birds' behaviour as part of the environment to which they respond, and the model is explained in more detail below. This speaks to the suggestion that the behaviour of con-specifics is a critical but neglected aspect of ethological work (e.g., Domjan *et al.*, 2000). In this framework, the behaviour of the chick can be accounted for by a series of presentations of discriminative stimuli and positive reinforcements produced by the adult gulls' behaviour. Considering Figure 4, the chicks' behaviours can be seen in the context of the adult gulls' behaviours, and vice versa, where each behaviour acts as the discriminative stimuli for the next

behaviour emitted by the conspecific, and the subsequent behaviour acts as the consequence for that conspecifics behaviour. Table 1 sets out the successive three-term contingencies for the behaviours that are presented schematically in Figure 4 and also identifies their setting events (discriminative stimuli) and maintaining events (consequences). To the extent that the sequence outlined in Table 1 is followed, then the behaviours will be maintained. However, as the various consequences for the behaviours alter, then this disrupts the next behaviour in the sequence, which, in turn, has implications for the next three-term contingency sequence.

 Table 1 about here

For the chick's initial response of approach or avoidance, the adult gulls' approach and call may be treated as the discriminative stimulus (see Charrier *et al.*, 2001). Early in the period observed in the current study, the chick's behaviour to the approaching adult appeared to be a well differentiated operant response – that is, one that was controlled by a particular adult, and the chick's approach to the adult gull and subsequent begging occurred mainly in the presence of the parent. In contrast, the chick tended to avoid the presence of alternative adult gulls. The approach and begging of the chick may well be maintained by the adult birds' settling in a receptive stance, and by display of the adults' bill. Possibly, this is due to the bill, and red spot, possessing secondary reinforcing properties due to their relationship with food. In terms of the chick's begging response (or bill pecking), the settled adult's bill serves as a discriminative stimulus (or Pavlovian conditional stimulus) for the chick to emit this

pecking behaviour. This pecking (or stimulus), in turn, is reinforced by the presentation of food by the adult gull. These patterns of chick behaviours altered over the course of the observation period in that the initially approach behaviour became less differentiated to one adult, and the begging response became more intense. These changes in the chick behaviours appear to be associated with changes in the adult responses to them (see below), suggesting a role for the three-term relationship in modulating these behaviours.

In terms of the adult gull's behaviour, this can be accounted for by a series of discriminative stimuli based on the chick's behaviour, and negative reinforcers provided by the chick's ceasing peeping. The initial arrival of the adult at the nest site is met by a 'peeping' response from juveniles, rather than aggression from other adults. This 'peeping noise might signal safety to the adult, and may serve as the discriminative stimulus for the adult's static 'receptive response' to the chicks. The adult's presentation of their bill, results in the termination of chick begging. This termination may serve as the maintaining consequence for the adult behaviour. Such juvenile sounds requesting food have been found to be aversive in humans (Shaw, 1977 Gross, Fredrickson, & Levenson, 1994), and there is evidence that noise, especially high-pitched noise, can be aversive in some species (Reed, Collinson, & Nokes, 1995).

As noted above, over the course of the observation period, this set of activities altered in two significant ways. Initially, the food requests on the part of the chicks started to become more intense, and begin to generalize toward adults other than the parents. These previously observed phenomena (see Graves *et al.*, 1991; Pugesek, 1990) may cause disturbance in the contingencies described above, and result in an alteration in parental behaviour. In particular, the parents' standing and bill presentation behaviour is

discontinued. There are a number of potential explanation for this behaviour. As the parents' standing is no longer followed by the cessation of the chicks' begging noise, which typically previously stopped when the parents' presented their bill and food, the parental behaviour is not maintained by this putative negative reinforcement, and it may alter to the extent that the chicks are no longer presented reliably with the bill. In fact, the parent tends to avoid the offspring. A reduction in the reinforcement for begging may result in an initial increase in this behaviour on the part of the chick. Both Lerman, Iwata, and Wallace (1999) and Zimmerman (1971) provide examples of extinction-induced increases in the rate of behaviour. Additionally, placing behaviour into extinction will widen the generalization of the response to other stimuli along the dimension, in this case to other adult gulls. In turn, this enhanced level of begging would serve further to reduce negative reinforcement for the parent. Alternatively, it may be that, as time goes by, the chicks' begging loses the power to induce parental offering – perhaps through habituation to the begging noise, hormonal changes in the adult, or visible maturational changes in the chick. In any case, the chicks' begging would lose its power as a discriminative stimulus. Whatever the explanation, it appears as if eventually, these contingencies would cause standing and bill presentation to extinguish in the parent.

There are two issues arising from this account of the change in behaviour over time that require comment. Firstly, it is argued that the removal of reinforcement (parental bill presentation) causes the chick to emit greater levels of peeping behaviour, but leads the adult, on removal of the negative reinforcement (cessation of 'peeping'), to show extinction of that bill presentation behaviour. This difference in the effect of

reinforcement withdrawal may reflect the suggestion that the chick's behaviour is positively reinforced by presentation of a conditioned reinforcer, whereas the parent's behaviour is aversively reinforced by the cessation of an aversive noise. It has been documented that extinction of a positively reinforced response initially can result in increased responding (Zimmerman, 1971), but there is little evidence that this is the case for negatively reinforced behaviour (e.g., see Galizio, 1999). Additionally, the chicks' behaviour is reinforced by a potential secondary reinforcer (the bill spot associated with food). It has been suggested that secondary-reinforced behaviour is much less sensitive to changes in contingencies than primary-reinforced behaviour (Holland & Rescorla, 1975).

Secondly, it is not entirely clear what might prompt the increase in chick feeding requests. The present report focused only on behavioural transactions between the parents and offspring. Of course, such increased begging could result from a reduction in food delivered by the parents, or a growing imbalance between energy needs and input provided by parental feeding. Certainly, the begging response is correlated with level of deprivation (Iacovides, & Evans, 1998), and this is one suggestion for the start of dispersal made by several theorists (see Kenward *et al.*, 1993).

It may be objected by adherents to the experimental analysis of behaviour, that the current study, although adhering to some principles of behaviour analysis, such as the three-term explanatory model, and analysis at the level of the individual, is not experimental in nature. Of course, this is true in that the study examined ecologically valid behaviour in context, and did not strive to manipulate any of the factors observed. However, there are two points that need to be made in response to this criticism. Firstly,

the purpose of this study was to examine the inter-dependency of behaviours of parent and offspring as they changed over time. Human intervention and manipulation may have dramatically altered these behaviours. Secondly, the factor usually designated as a confounding variable in the experimental analysis of behaviour (i.e. the passage of time) was the independent variables to be studied in the present report. The other behavioural interactions noted were examined as a function of this variable. Thus, in this study it can be said that a critical factor (time) was varied, but not (of necessity) manipulated by the experimenter.

It should be noted that although time was a critical factor in the development sequence noted in this study, the selection of the particular period during which to observe the gulls was fortuitous. Observation proper began after two days of observing the gulls, and noting invariant behavioural patterns that seemed to be interesting. Otherwise, there were no criteria applied as to when to begin the observation. This was serendipitous for the current study, however, further work might be directed at identifying precisely when this sequence might begin, and whether there are any individual and environmental impacts on its structure or initiation.

In summary, the current report replicated and extended several previous observations regarding parent-offspring behaviour. These were the increase in begging and decrease in parental feeding over time. It also documented a novel change in behaviour (widening of the range of adult birds chicks would beg from). Importantly, these activities were interpreted as functions of one another. Of course, these observations need to be extended, and the predictions of the model tested under different conditions (perhaps, even experimentally). Nevertheless, the above description of the

parent-offspring gull behaviour is offered in the spirit of Skinner's suggestion regarding an interpretation of behaviour within a radical behaviourist framework. It also represents an attempt to treat the behaviour of the individuals as part of the proximal causes of parent-offspring conflict and dispersal.

5. References

- Asaduzzaman, S. M., & Wild, G. (2012). The evolution of dispersal conditioned on migration status. *Ecology and Evolution*, **2**, 822-843.
- Baerends, G.P. (1985). Do the dummy experiments with sticklebacks support the IRM concept? *Behaviour*, **93**, 258-277.
- Baaloudj, A., Samraoui, F., Laouar, A., Benoughidene, M., Hasni, D., Bouchahdane, I., ... & Samraoui, B. (2012). Dispersal of yellow-legged gulls *Larus michahellis* ringed in Algeria: a preliminary analysis. *Ardeola*, **59**, 137-144.
- Baum, W.M., & Aparicio, C.F. (1999). Optimality and concurrent variable-interval variable-ratio schedules. *Journal of the Experimental Analysis of Behavior*, **71**, 75-89.
- Charrier, I., Mathevon, N., Jouventin, P., & Aubin, T. (2001). Acoustic communication in a black-headed gull colony: How do chicks identify their parents? *Ethology*, **107**, 961-974.
- Clobert, J., Baguette, M., Benton, T. G., Bullock, J. M., & Ducatez, S. (2012). *Dispersal ecology and evolution*. Oxford University Press.
- Crawford, L.L. (1986). Behavior analysis takes a field trip. A review of Krebs' and Davies' Behavioral Ecology: An Evolutionary Approach. *Journal of the Experimental Analysis of Behavior*, **46**, 395-411.
- Davis, J., & Quinn, J.S. (1997). Distribution of parental investment and sibling competition in the herring gull, *Larus argentatus*. *Behaviour*, **134**, 961-974.
- Dickinson, J. L., & McGowan, A. (2005). Winter resource wealth drives delayed dispersal and family-group living in western bluebirds. *Proceedings of the Royal*

- Society B: Biological Sciences*, **272**, 2423-2428.
- Domjan, M. (1994). Formulation of a behavior system for sexual conditioning. *Psychonomic Bulletin & Review*, **1**, 421-428.
- Domjan, M., Cusato, B., & Villarreal, R. (2000). Pavlovian feed-forward mechanisms in the control of social behavior. *Behavioral and Brain Sciences*, **23**, 235-282.
- Galizio, M. (1999). Extinction of responding maintained by timeout from avoidance. *Journal of the Experimental Analysis of Behavior*, **71**, 1-11.
- Graves, J., Whiten, A., & Henzi, S.P. (1991). Parent-offspring conflict over independence in the herring gull (*Larus argentatus*). *Ethology*, **88**, 20-34.
- Griffin, A. S., & Galef, B. G. (2005). Social learning about predators: does timing matter? *Animal Behaviour*, **69**, 669-678.
- Gross, J.J., Fredrickson, B.L. & Levenson, R.W. (1994). The psychophysiology of crying. *Psychophysiology*, **31**, 460-468.
- Hailman, J.P. (1969). How an instinct is learned. *Scientific American*, **221**, 98-106.
- Holland, P.C., & Rescorla, R.A. (1975). The effect of two ways of devaluing the unconditioned stimulus after first- and second-order appetitive conditioning. *Journal of Experimental Psychology: Animal Behavior Processes*, **1**, 355-363.
- Iacovides, S., & Evans, R.M. (1998). Begging as graded signals of need for food in young ring-billed gulls. *Animal-Behaviour*, **56**, 79-85.
- Jensen, P. (2001). Parental behaviour. In, L.J. Keeling & H.W. Gonyoul (Eds.), *Social behaviour in farm animals* (pp. 59-81). Cab International.
- Kenward, R.E., Marcstroem, V., Karlbom, M. (1993). Post-nestling behaviour in goshawks, *Accipiter gentilis*: I. The causes of dispersal. *Animal-Behaviour*, **46**,

- 365-370.
- Korpimäki, E., Salo, P., & Valkama, J. (2011). Sequential polyandry by brood desertion increases female fitness in a bird with obligatory bi-parental care. *Behavioral Ecology and Sociobiology*, **65**, 1093-1102.
- Lerman, D.C., Iwata, B.A., & Wallace, M.D. (1999). Side effects of extinction: Prevalence of bursting and aggression during the treatment of self-injurious behavior. *Journal of Applied Behavior Analysis*, **32**, 1-8.
- Mackintosh, N.J. (1983). *Conditioning and associative learning*. Oxford: Oxford University Press.
- Morales, J., & Velando, A. (2013). Signals in family conflicts. *Animal Behaviour*, **86**, 11-16.
- Pellon, R., & Blackman, D.E. (1987). Punishment of schedule-induced drinking in rats by signaled and unsignaled delays in food presentation. *Journal of the Experimental Analysis of Behavior*, **48**, 417-434.
- Pierotti, R., & Annett, C. (2001). The ecology of Western Gulls in habitats varying in degree of urban influence. In *Avian Ecology and Conservation in an Urbanizing World* (pp. 307-329). Springer US.
- Pierotti, R.J. & Good, T.P. (1994). Herring Gull (*Lams argentatus*). In A. Poole & F. Gill (Eds.), *The birds of north America*, 124. Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.
- Plotkin, H. (2002). Intelligence as predisposed skeptical induction engines. In R.J. Sternberg & J.C. Kaufman (Eds.). *The evolution of intelligence* (pp. 339-367). Mahwah, NJ: Lawrence Erlbaum Associates.

- Pugesek, B.H. (1990). Parental effort in the California gull: Tests of parent-offspring conflict theory. *Behavioral Ecology and Sociobiology*, **27**, 211-215.
- Reed, P., Collinson, T., & Nokes, T. (1995). Aversive properties of auditory stimuli. *Learning and Motivation*, **26**, 101-115.
- Seligman, M.E.P., & Hager, J.L. (1972). *Biological boundaries of learning*. East Norwalk, CT: Appleton-Century-Crofts.
- Shaw, C. (1977). A comparison of the patterns of mother-baby interaction for a group of crying, irritable babies and a group of more amenable babies. *Child Care, Health and Development*, **3**, 1-12.
- Skinner, B.F. (1969). *Contingencies of reinforcement: A theoretical analysis*. New York: Appleton-Century-Crofts.
- Timberlake, W. (1993). Behavior systems and reinforcement: An integrative approach. *Journal of the Experimental Analysis of Behavior*, **60**, 105-128.
- Timberlake, W. (1994). Behavior systems, associationism, and Pavlovian conditioning. *Psychonomic Bulletin & Review*, **1**, 405-420.
- Tinbergen, N., & Perdeck, A.C. (1950). On the stimulus situation releasing the begging response in the newly hatched Herring Gull chick (*Larus argentatus argentatus* Pont.). *Behaviour*, **3**, 1-39.
- Tinbergen, E.A., & Tinbergen, N. (1972). *Early Childhood Autism: An Ethological Approach*. New York: Taylor Francis.
- Trivers, R.L. (1974). Parent-offspring conflict. *American Zoologist*, **14**, 249-264.
- Watson, J.B. (1908). The behavior of noddy and sooty terns. *Carnegie Publications*, **103**, 187-255.

Zimmerman, D.W. (1971). Rate changes after unscheduled omission and presentation of reinforcement. *Journal of the Experimental Analysis of Behavior*, **15**, 261-270.

6. Acknowledgements

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7. Figure Captions

Figure 1. Types of chick response to the approach of an adult bird expressed as a percentage of all behaviours after the adult's approach over 7 successive days (2 sessions a day). Par-app = parental approach; Par-av = parental avoidance; other-app = approach of nonparent gulls; other-av = avoidance of nonparent gulls.

Figure 2. Parental adult responses to the approach of a chick bird expressed as a percentage of all behaviours after the chick's approach over 7 successive days (2 sessions a day).

Figure 3. Parental adult responses to the begging behavior of a chick expressed as a percentage of all behaviours after the chick's approach over 7 successive days (2 sessions a day).

Figure 4. Schematic representation of the gull behavioural feeding sequence, and these behaviours role in successive three-term contingencies.

Table 1: Setting events (discriminative stimuli) and maintaining events (consequences) for chick and adult behaviours over the course of the feeding sequence.

Setting event	Behaviour	Maintaining event
Adult arrival	Chick approach	Adult receptive stance
Chick approach	Adult receptive stance	Cessation of chick approach
Adult receptive stance	Chick begging	Adult food presentation
Chick begging	Adult food presentation	Cessation of chick begging

Figure 1

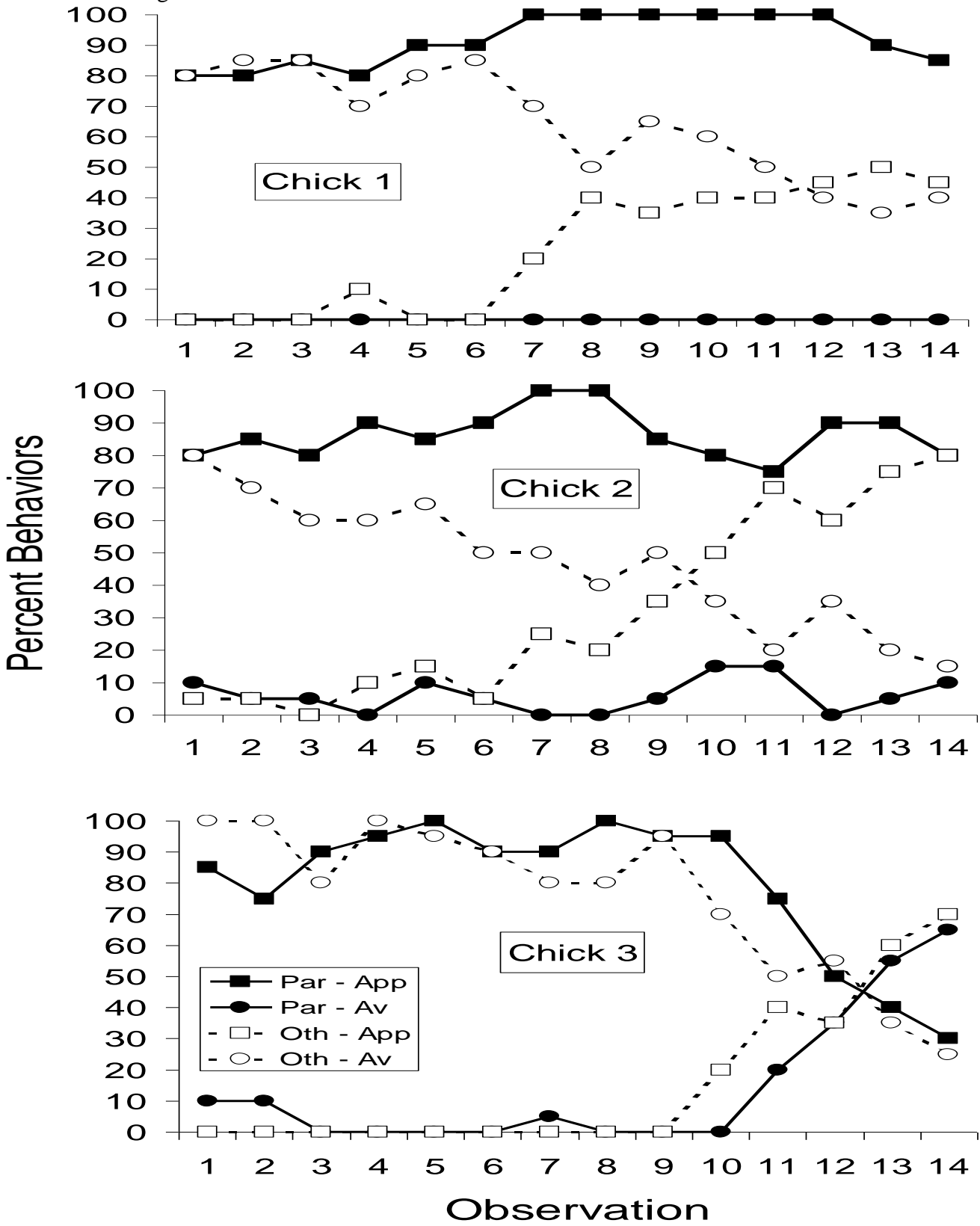
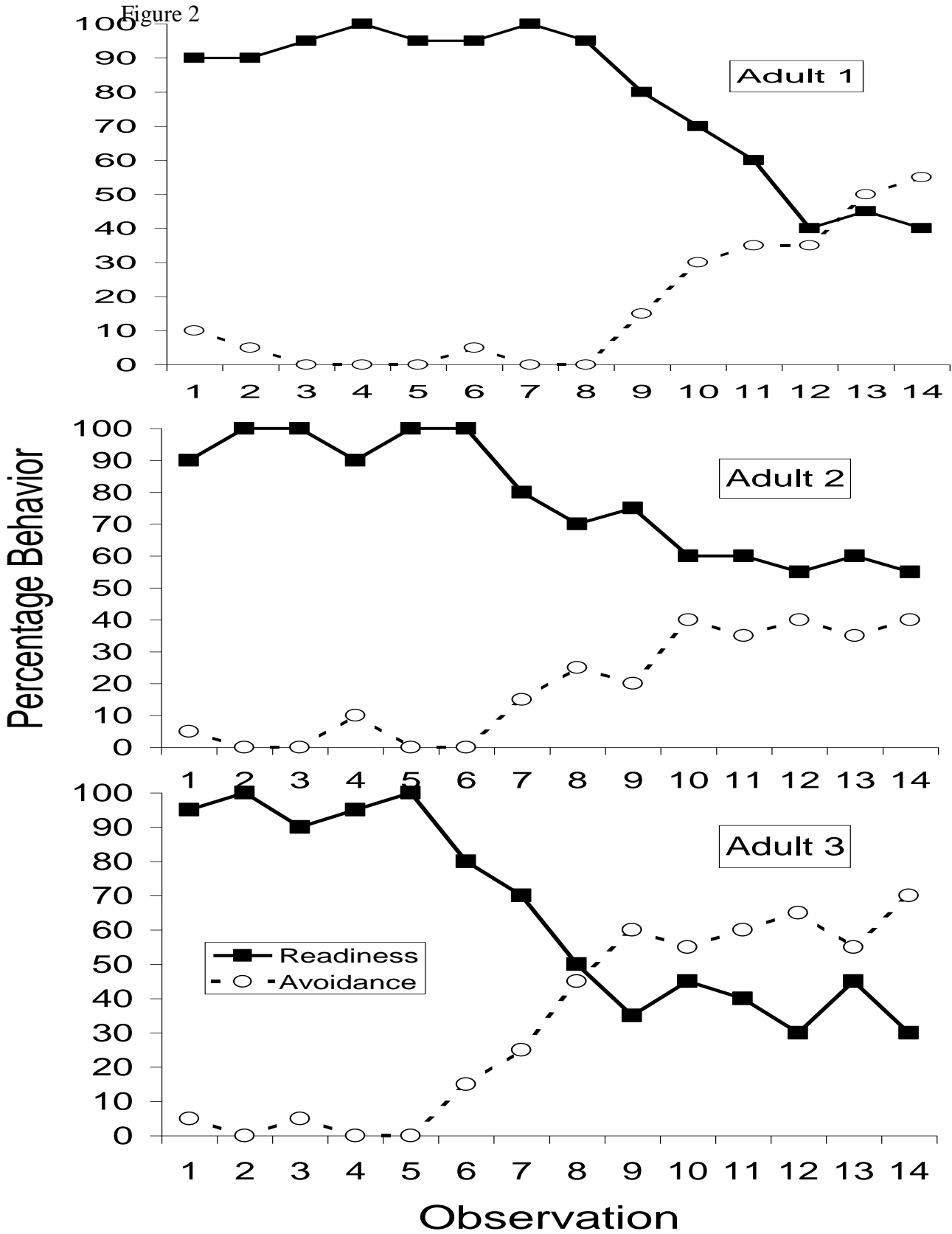


Figure 2



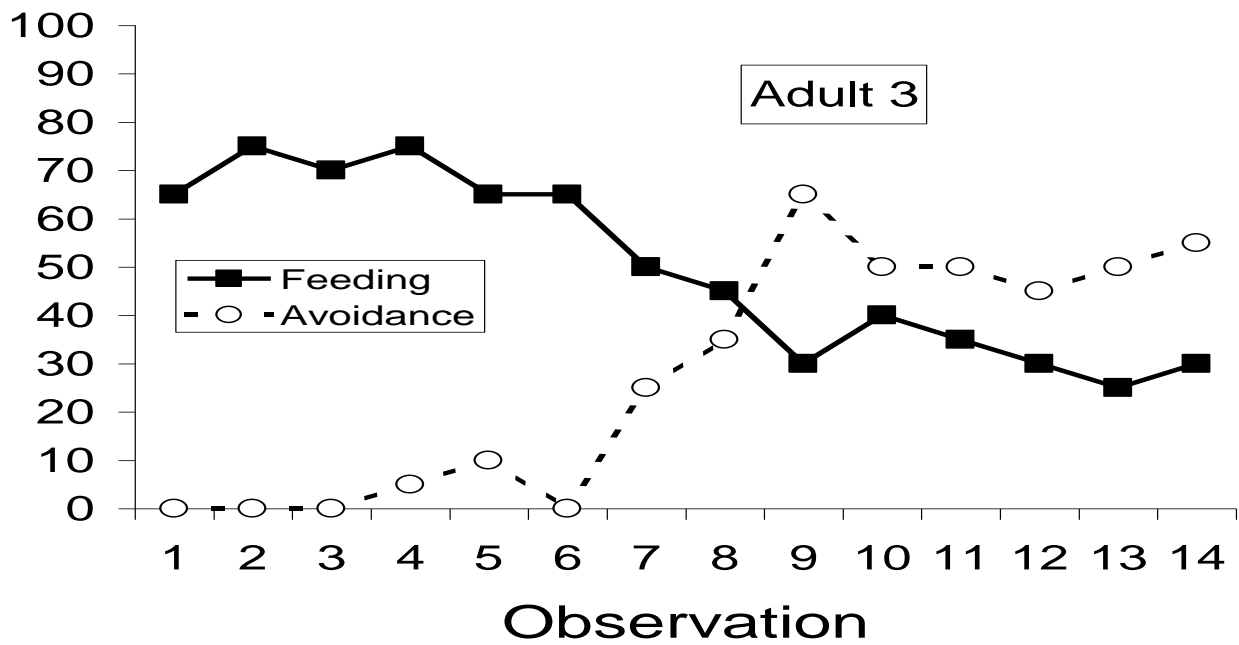
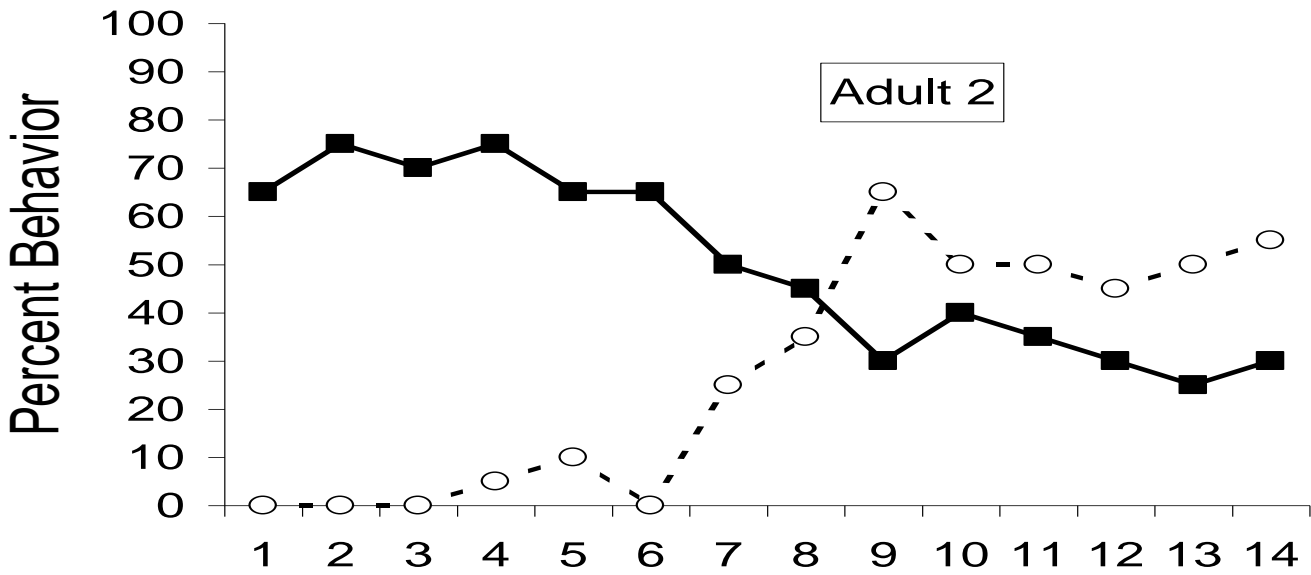
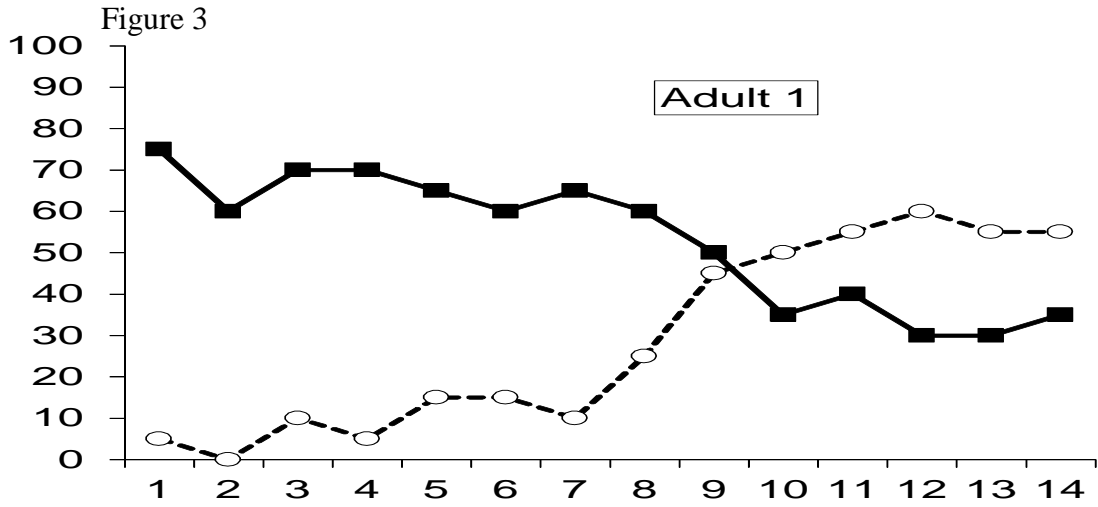


Figure 4

