Behavioral Studies

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ETHOLOGY: THE SCIENTIFIC APPROACH TO ANIMAL BEHAVIOR

A flying raptor is fascinating. Whether you are observing an eagle's display flight, an aerial transfer of food between two courting harriers, or a successful hunt by a Verreaux's Eagle (*Aquila verreauxii*), each is an impressive experience. Beyond the aesthetics of these displays lie many things that are of interest to biologists. Most of these deal with the ecological aspects of raptor biology, others with behavioral aspects. The latter, in particular, remain unstudied among raptor biologists.

This chapter provides raptor biologists with an introduction to behavior-study techniques, including methods and equipment used for descriptive and experimental analysis of behavior, both in the field and in the lab.

Some Introductory Concepts

Ethology, or Comparative Psychology, is a relatively young but growing discipline. Its name, literally, means "the study of behavior." Ethology usually is considered the legacy of Konrad Lorenz, Niko Tinbergen, and a few other animal behaviorists. The mark that these early investigators made on this discipline was that behavior is a product of natural selection, just like any phenotypic character. Natural selection acted, in the past, in shaping the behavior that is now observed in the present. Therefore, in ethological studies, it is important to consider the behavior in relation to its adaptive function in each species. Consequently, behavior usually can be better understood in free-ranging animals than in captive individuals.

The study of behavior's proximal causes was the start of a vigorous debate between North American animal behaviorists, who concentrated on the possibility of behavior modification (i.e., the ability to learn) rather than natural selection, and European ethologists, who speculated about causation and experimentally tested the adaptive function of specific behavior. After several decades the debate was settled, as both schools realized that all behavior, being the result of evolution, is comprised of both innate and experiential components.

Formulating the Hypothesis

Raptor biologists should keep in mind that the behavior of the birds they study is a central aspect of their biology and that behavior has the same degree of importance as other biological and ecological patterns. The seemingly limited repertoire of active behavior patterns displayed, interrupted by long periods of inactivity, can lower the appeal of behavioral studies. However, as any patient observer will soon realize, birds of prey display many types of behavior, and the study of ethology is critical to understanding the biology of raptors.

Before setting up an ethological study, the researcher must determine the experiment's starting point as well as its goals. Although the behavior itself is what an individual does, an ethological study should not restrict itself to the simple description of which behaviors are displayed, but also should ask questions regarding what, who, why, where and when the patterns in question occur (Lehner 1996).

What is simply an accurate description of behavior, which is made up of a sequence of behaviors. Taken together, these behaviors form the behavioral repertoire of individuals performed in particular contexts, roughly corresponding to what ethologists call an ethogram. Today this is considered to be a list of behaviors displayed by a certain species, or a behavior repertoire.

Who refers to the identification of the individual performing the behavior. This is important, not simply to avoid repetitive recordings, but because behavior can differ between and within sex, age class, and species. It also is important to know the identity of individuals near the bird performing the act, as well as the entity to whom that act is directed.

How refers to the description of the motor patterns used by the individual to perform a goal-oriented behavior, such as how to fly from one perch to another.

Why refers to either motivation or adaptation. Motivation refers to the individual performing the behavior, whereas adaptation has an evolutionary or ecological implication. Although seemingly separate concepts, they often are connected.

Where deals with the spatial aspect of the behavior. It refers to the geographic location where the behavior is performed, the location within the ecosystem, or the relative position of the individual performing the behavior in relation to other individuals.

When refers to the temporal component of the behavior. It includes the frequency of occurrence with respect to day, year, and lifetime, as well as timing of such a pattern within a behavioral sequence.

The "what" question usually is the starting point of any ethological investigation, but generally all of the questions above should be addressed. Whereas the "where" and "when" questions tend to follow the "what" question logically enough, the "how" and, above all, "why" questions often are the most difficult to answer. What follows provides an overview of the steps needed to collect useful information for behavioral studies.

DATA COLLECTION

In order to test hypotheses and achieve the study's goals it is essential that you obtain data that can be analyzed statistically and compared with those of other researchers. Therefore, it is necessary to assess and to plan precisely what you will study and how you will do so before starting data collection.

Level of Investigation

The choice of what to study ranges from the analysis of various types of behavior exhibited by one species to the analysis of a specific behavior in several species. In both cases, the study species should have some basic characteristics (Lehner 1996) including:

Suitability. The species must perform behavior patterns in a repeated, observable way. Suitability is increased if birds are individually recognizable or are marked to make them so.

Availability. Individuals must be accessible and observations should be carried out without affecting behavior. If the study involves captive individuals, the appropriate permits must be obtained for trapping or holding them in captivity.

Adaptability. If the study requires captivity, the species must be able to adapt to this context without altering the behavior in question.

Background information. The researcher must do a thorough literature search on the species to know how to best approach individuals and how to plan the study.

Based on the study's goals, the researcher should decide whether to conduct the study in the wild, in captivity, or both. In studies involving captive individuals, the researcher can manipulate the environment and control many variables. However, there is the risk of alterations in behavior due to the unnatural environment. In contrast, the researcher can observe a natural behavior in its entirety when studying the subject in the wild, but has to adapt to the animal's rhythm or activity cycle, and might not to be able to control the often numerous natural variables. Both studies in captivity and in the wild have disadvantages and advantages, and it is ideal to study a behavior or species in both circumstances.

One also should decide whether to simply describe the behavior (a **descriptive study**) or to collect data to test one or more hypotheses (an **analytic study**). If the latter, it is necessary to decide whether to collect data by simple behavioral observations (a **measurative study**) or by means of environmental or animal manipulation (a **manipulative study**), or both. There are many intermediate situations between these two extreme situations. In fact, Lehner (1996) points out that, *"we can categorize ethological research along a continuum from* *descriptive field studies to manipulative laboratory experiments."*

Before beginning the study, the researcher should consider carefully which methods to use. Below, we list a series of recording and sampling rules to help in the choice concerning how to carry out a study. These rules can be used in ethological research, in both descriptive and in measurative and manipulative analytical studies.

Describing Behavior

In every ethological study, the description of a behavior must be clear and precise in order to obtain data that are comparable with those collected by other researchers. Therefore, before beginning the study, it is important to choose *a priori* the behavioral categories to observe and record, and to define them clearly and precisely. A preliminary study and the drawing of an ethogram can be a great help. A good example of an actigram — or standardized form of an ethogram — for raptors can be found in Walter (1983). Martin and Bateson (1993) suggested that it is also important to consider that two types of behavior patterns can be identified:

An "**event**" is a relatively brief behavior pattern, such as a discrete body movement or vocalization, which can be approximated as a point in time. Often, the most relevant feature of an event is its frequency of occurrence.

A "**state**" is a relatively long behavior pattern, such as a prolonged activity, body posture or proximity measure. Often, the most relevant feature of a state is its duration.

Choice of behavioral categories. Each behavior is represented by a continuum of several movements and postures, making it difficult to obtain a definitive measurement. Consequently, before starting to collect data, it is often advisable to split any behavior into categories in order to make collection easier and more precise. For example, to describe and measure the hunting behavior of a bird of prey, it is better to divide this activity into its various components: prey search, pursuit, capture, manipulation, and ingestion. Although the type and number of categories are related to the type of behavior, the study's goals, and the level of investigation, Martin and Bateson (1993) suggested features that should characterize these categories:

Number. The number of categories should provide a sufficiently detailed description of the behavior in relation to the research goals.

Definition. Each category should be defined in a clear, precise, and comprehensive way, describing what is meant to be included in that category (ostensive definition) and describing the method used to measure it (operational definition).

Independence. The categories should be independent, so that each behavior pattern can be ascribed to only one category.

Homogeneity. All behavior patterns assigned to the same category should exhibit the same properties.

Cresswell (1996) defined behavior patterns in his study on Eurasian Sparrowhawks (*Accipiter nisus*), Peregrine Falcons (*Falco peregrinus*) and Merlins (*F. columbarius*) very precisely:

> *"(1) Hunting. Purposeful flight in an area of potential prey in a manner that led to, or could potentially lead to, an attack. For Sparrowhawks, this was rapid low contour-hugging, an approach flight that used cover or direct dashes at prey. For Peregrines, this included any flight through, or with, groups of prey, except when the potential prey was mobbing. For Merlins, it included only periods of flight in which attacks were recorded.*
> *(2) Hunting/moving. Any flight in an area of potential prey that could not be classified as hunting. Merlins, for example, would use the same very low and rapid hunting flight to move between perches between long periods of activity as well as during definite hunting periods with many attacks.*
> *(3) Perching. Either on the ground or on an object. Perching did not include any time spent feeding or caching prey.*
> *(4) Feeding. Plucking or eating prey."*

Types of behavioral description. There are basically two types of behavioral descriptions (Martin and Bateson 1993, Lehner 1996): empirical and functional descriptions.

An **empirical description** (i.e., a description based on structure) describes the behavior according to how it is subdivided, annotating a series of postures and body movements. An example is "the Golden Eagle (*A. chrysaetos*) flies, maintaining its wings open and still." This type of description is particularly useful during preliminary studies and when drawing up ethograms. However, it can be redundant and of little use in the other contexts.

A **functional description** (i.e., a description based on the function) describes the behavior according to the functional outcome that follows a series of postures and movements. An example of description based on function is "the Golden Eagle is gliding." Caution should be exercised, however, as a functional description can induce the observer to subjectively interpret observed behavior. Using the previous example, an observer could write, "the Golden Eagle is in a hunting glide" or simply "the Golden Eagle is hunting," attributing purpose to the Golden Eagle's behavior. Interpreting the aim of the behavior during data recording sometimes results in incorrect or incomplete information and can create confusion during data processing. During the description of a behavior, it is very important that the researcher does not attribute adjectives or definitions that can implicitly or explicitly give an indication of the behavior's causes or aims.

Although the distinction between these two behavioral descriptions is important, it is not always clear, and it is sometimes appropriate to use both description types within the same study.

Sampling Rules

Sampling is at the core of any ethological study. The sampling rules used depend on several variables specific to each study. These include the experimental design, the type of behavioral unit (events, states, or both) to be recorded, the observational accuracy available, and, above all, the research question.

Ad libitum sampling. This method is useful to record events and states. In fact, this sampling rule allows the researcher to record all behavior patterns exhibited during the sampling period by all individuals visible during that period. In other words, the researcher records all that is observable, without limitation to the number of subjects or behavior patterns seen. The recording of all that is observable has two problems. The first is that the observer will be inclined to record the more frequent and more striking behaviors (i.e., those attracting attention more than others), whereas they may overlook rare behavior. The second problem is that this method is very exacting. This sampling rule is of little use for collecting quantitative data, but is particularly useful during preliminary studies, or when compiling an ethogram.

Focal-animal sampling. This method involves recording the occurrence and the duration of all types of behavior patterns exhibited by a single focal individual. In this case, the limiting factor is that only one individual is observed, whereas there is no restriction on the number of behaviors recorded. Sometimes the researcher may choose to record the behaviors of a focal-pair or a focal-group, but at such times recording can become more difficult and the researcher runs the risk of not recording important information. Focal individuals can be chosen randomly or on the basis of certain characteristics. The focal-animal sampling method is useful for recording both events and states. Tolonen and Korpimäki (1994) studied parental effort in several pairs of Common Kestrel (*F. tinnunculus*) using this method. Behavioral categories tied to male activity (sitting, directional flight, active flight-hunting and soaring) were recorded by using continuous observation of each focal male for 6–8 hours during courtship and incubation, or for 4–6 hours during the nestling period.

All-animal sampling. With all-animal sampling, the observer records the occurrence of a certain behavior or a category of behaviors exhibited by a group of individuals. Thus, the limiting factor is the number of behavioral event or states to observe, whereas there is no restriction on the number of individuals. This method can be used to record both events and states. Sergio (2003) assessed the effect of weather on the foraging performance of Black Kites (*Milvus migrans*) by observing the entire colony and recording each hunting attempt, and relative outcome, during each observation session.

Recording Rules

Within a study, a one-sampling rule (focal-animal sampling, all-animal sampling, or *ad libitum* sampling) is usually combined with one of the following recording rules (continuous-recording sampling or time sampling).

Continuous-recording sampling. This involves several methods consisting of recording various parameters of a behavior or behavioral categories during a specific sampling period: time of beginning and ending, sequence and duration. The data obtained are numerous and precise, and the effort required by the observer is quite high.

All-occurrences sampling. This method is also called "event-sampling" or "complete record sampling." It records the frequency and the rate of all occurrences of a certain behavior or behavioral category. Usually, it is used to record events, and is useful to assess synchrony or the rate of an easily observable behavior pattern that does not occur frequently. Given the practical difficulty of recording all occurrences of specific behaviors or states, the all-occurrences sampling method is often associated with focal-animal sampling. An example is seen in Mougeot (2000), where territorial intrusions and copulation patterns in 26 pairs of Red Kites (*M. milvus*) were investigated. During each observation period, which lasted on average 1.6 hours, Mougeot observed one focal pair, continuously identifying and recording the occurrences of various behavior patterns (interaction with conspecifics, copulation, male prey deliveries, time spent by male and female within the breeding territory).

Sequence sampling. Sequence sampling is mainly used to study behavior patterns, displayed by an individual, pair, or group in sequence (e.g., courtship displays, hunt displays). During sequence sampling, the observer records all behavior exhibited, noting time and frequency of individual events and states. Usually, the start and end of each sequence-sampling period is determined by the start and end of the sequence. Sampling duration must be chosen in relation to the type and occurrence frequency of the behavioral sequences. This method can be used to record both events and states. Edut and Eilam (2004) studied the protean behavior of the social (Guenther's) vole (*Microtus socialis*) and of the common spiny mouse (*Acomys cahirinus*) under Barn Owl (*Tyto alba*) attack. Within each 3-hour test period, the continuous recording of both owl and rodent behavioral sequences started on the first owl attack and ended with the capture of a rodent.

Sociometric matrix. This is a method for tabulating data useful for measuring the synchrony and sequence of behaviors of individuals in a group. Csermely and Agostini (1993) investigated the social and agonistic interactions of an acquainted group of rehabilitated Barn Owls. They identified and recorded seven behaviors displayed by the active bird (initiator) in the interaction and eight behaviors displayed by the passive bird (recipient). Each interaction was characterized by the dyads of behavior performed by both initiator and recipient birds. Interactions could then be summed in a matrix of 56 (7 x 8) cells (Table 1). The matrix usually is read from left to right, with the frequency of the initiator's behavior listed in rows and that of the follower in columns.

It is important to keep in mind that the sociometric matrix is a method used only to organize data and is not the same as a contingency table, despite their similar appearances.

Time sampling methods. These methods consist of recording behavioral events periodically, instead of continuously, during the sampling period. The sampling period is usually subdivided into several intervals during which behaviors are recorded. These methods col-

Table 1. An example of a sociometric matrix using data from Csermely and Agostini (1993). The behaviors considered for the initiating bird are listed in the column on the left and those for the recipient bird in the heading across the top. In this example, each cell indicates the frequency of the behavior transition recorded for each interaction. For instance, the interaction in which the initiating bird displaced the recipient bird, which reacted with physical contact (PC), was recorded eight times. A total of 202 interactions was recorded in this session. (TH, threatening; AP, approach; AL, allopreening; PC, physical contact; DI, displacement; BB, beak-beak contact; AG, aggression; RE, retreat; NR, no reaction.)

BEHAVIOR	TH	AL	PC	DI	BB	AG	RE	NR	TOTAL
Threatening	0	0	0	0	1	0	1	4	6
Approach	2	3	7	0	18	3	0	0	33
Allopreening	0	7	0	0	5	0	0	23	35
Physical contact	0	0	0	1	4	1	5	26	37
Displacement	0	3	8	0	2	1	3	11	28
Beak-beak contact	0	2	3	0	0	0	19	31	55
Aggression	0	0	0	0	0	0	6	2	8
TOTAL	**2**	**15**	**18**	**1**	**30**	**5**	**34**	**97**	**202**

lect less information than continuous-recording sampling methods, but they are less demanding of the observer, are particularly useful if the observer is not an expert, and also allow the observation of several subjects or behavior at the same time.

One-zero sampling. This method is also called "fixed-interval time-span sampling" or the "Hansen system." The observer scores whether a certain behavior occurred (1) or not (0) during very short sampling intervals of 10 to 60 seconds each, in which the observation period is split. This method can be used to record both events and states, but is usually used to record states and, above all, to study behaviors that begin and end quickly. The length of the sample intervals and the time between sampling intervals must be chosen carefully with respect to the type of behavior or behavioral categories studied. Usually, the shorter the sample interval, the more accurate is the documentation of the behavior in question. Because the simultaneous recording of many behavioral categories is difficult, the length of the sampling interval will be a compromise between length of the observation and number of behavior patterns recorded. The greater limitation of this method is that it does not measure actual frequency and duration. It is worth noting that some authors (e.g., Altmann 1974) believe that this method should not be used because it is not always reliable.

Instantaneous and scan sampling. Instantaneous sampling also is called "point sampling," "fixed-interval time point sampling," "on-the-dot sampling," or "time sampling." The observer records the behavior displayed by one individual at a fixed point sampled within the sampling period. This method is useful for recording states, but not events because both events and time-points are instantaneous and it is unlikely that they will occur at the same time.

Scan sampling is a form of instantaneous sampling where the observer records the behavior displayed by several individuals at fixed-point samples. This method is important to estimate the percentage of time that an individual spends in particular activities. In a laboratory experiment, Palokangas et al. (1994) tested whether female Common Kestrels preferred brightly ornamented males. Each female had to choose between two males caged in front of her. During the 15-minute tests, the researcher recorded which male the female was looking at every minute.

Regardless of the method, it is important that the duration of each sampling is always the same to allow the comparison with other data collected by the researcher with data in other ethological studies. The length of the sampling period depends on the type of behavior studied and on its frequency of occurrence. If, during the sampling period, the subject is out of sight of the observer, it is necessary to estimate this duration and to consider it during data processing. When this occurs, we suggest consulting the guidelines proposed by Lehner (1996).

Finally, it is necessary to emphasize that it is a good idea to carry out preliminary observations before choosing sampling and recording methods in order to have an accurate overview of which behaviors to study. Moreover, during the first phase of data collection, the recording observer's efficiency tends to improve (observer drift; Martin and Bateson 1993). Consequently, it is advisable to familiarize yourself with the collection method before beginning the experiment. This will help mitigate the possibility of changing data reliability over the course of the study.

Once the data have been collected, it may be very difficult to explain why a behavior is displayed. Animal behavior is affected by many factors including habitat, season, hormones, genetics, and phylogeny. Consequently, when planning an ethological study, the researcher has to take these factors into account.

EXAMPLES OF DATA COLLECTION IN THE FIELD AND IN CAPTIVITY

There are many different ways to investigate the behavior in birds of prey. Every species has its own set of adaptations and can respond differently to the same environmental stimulus. This section reviews the tools that can be used to study raptor behavior both in the wild and in captivity. This section is not exhaustive, and should be considered introductory for those who wish to set up an ethological study.

Mate Choice

Mate choice is one of the most investigated behaviors in ethology. In most studies, the attention focuses on female choice, but, nevertheless, it is important to know which factors affect male choice, principally in monogamous species, where both partners are involved in parental care, and which often is the case in birds of prey.

Mate choice can be influenced by several of the partner's characteristics: age, phenotype (e.g., body

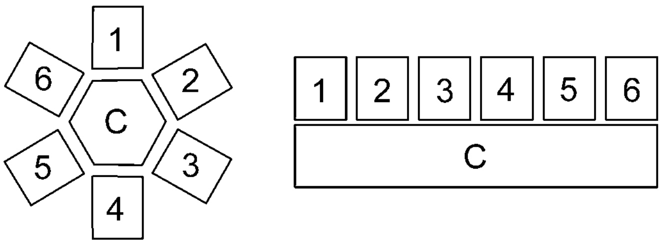

Figure 1. An experiment investigating mate choice in which a bird in cage C "chooses" among birds in cages 1–6. The choice can be assessed in each situation by measuring which bird looked toward or "visited" longer or more frequently than the others.

size, body symmetry, plumage color and brightness), parasite load, hunting efficiency, territory characteristics, etc. However, because most of these factors are interrelated (e.g., territory quality and hunting efficiency, plumage brightness, general health, and parasite load, etc.), it is necessary to consider these relationships when designing the study so as to distinguish the influence exerted by each factor and to draw the correct conclusions.

In works conducted in the wild, it may be necessary to tag the individuals with proper identification (e.g., using color rings, wing-tags, dyed feathers, or radio-transmitters) and to gather morphometric data, physiological (e.g., blood) samples, or both. Capturing birds of prey and tagging them are discussed in detail in Chapters 12 and 13.

Standardized observations (focal-animal sampling or all-animal sampling) allow the researcher to verify if certain behaviors affect mate choice. Village (1985) recorded the individual arrival dates of a Common Kestrel population arriving in spring. All birds were tagged and aged (first-year or older) in previous years in order to recognize them and to distinguish migrants from over-wintering kestrels. The date when the last-arriving partner was seen for the first time was considered the date of pairing. Pairing dates revealed assortative mating based on age and arrival time in each territory.

Tagging of individuals also helps record the possible occurrence of extra-pair copulations or polygamy (polygyny or polyandry), which are important factors to be considered in mate-choice studies.

Although courtship in birds of prey often involves acrobatic display flights, and whereas mate quality is evaluated on the basis of several factors, including male hunting skill, mate preference can be examined in captivity as well. The experimental structure for doing so usually consists of several cages, one containing the "choosing bird" and, in front of it, several others containing the birds to be evaluated and chosen. The latter cages are either in a row or in a radial position (Fig. 1). The choice can be made by simply visiting each cage or, in the second case, by turning the body to watch the preferred mate. Such a test is ultimately a replication of lek behavior displayed by many animals (Höglund and Alatalo 1995).

Individuals are evaluated based on body characters or behavior. In each case, it is important to limit the number of variables by which individuals differ. Palokangas et al. (1994) tested the Common Kestrel female's preference for brightly feathered males. The test was carried out in a room divided by a wall; each half contained one male, unable to see the other. The female was placed in a small box in the middle of the test room and was able to see the males through a one-way window from the box. Each female had 15 minutes in which to evaluate both males. During this time the researchers recorded which male the female was looking toward every minute (instantaneous sampling).

Parental Care

Because most of them are monogamous and raise altricial nestlings, birds of prey can be interesting subjects when it comes to parental care and parental effort. To quantify parental care several variables should be measured: parental and offspring survival over time, time spent by parents incubating the eggs and brooding the young, food provisioning rate (measured as the number of prey items delivered to the nest per time unit), and defense behavior. Tolonen and Korpimäki (1995) studied the nest defense behavior of Common Kestrels towards a stuffed pine marten (*Martes martes*) placed under a cover on a nest box roof. After removal of the cover, defense behavior was recorded for 5 minutes, with the activity of the male and female recorded separately. The intensity of the behavior, classified into six categories, was evaluated, and data recording started when at least one member of the pair overtly reacted to the predator.

Social Behavior

Some raptors are social or at least gregarious. Some, including Eleonora's Falcon (*F. eleonorae*), exhibit social feeding strategies, others, including Lesser

Kestrel (*F. naumanni*), nest in colonies, and still others, including Red Kite, roost communally. Any study focusing on social behavior requires individual recognition, either by plumage characteristics or by markers (color rings, wing-tags, dyed feathers, or transmitters for radio-tracking). Hiraldo et al. (1993) tagged 46 Red Kites wintering in communal roosts with radio- and wing-tags and defined four categories of individuals on the basis of age (young or adult) and status (wintering or resident), and then conducted all-animal sampling to determine the time of departure from the roost, the flight direction, whether kites flew alone or in groups, and if there was a group leader. The researchers considered feeding duration from the previous day as the basis for their foraging success: high success for more than 30 minutes of feeding and low success for less than 5 minutes of feeding. The data recorded did not confirm the hypothesis that roost sites act as food information centers (i.e., sites where kites get information from mates about food locations [cf. Ward and Zahavi 1973]).

In captivity, such as during physical rehabilitation, birds of prey often can be kept in groups without showing apparent behavioral alterations due to unnatural density. In this context, a detailed analysis of their behavioral repertoire and the behavioral transitions occurring when birds interact is a useful tool to anticipate negative effects of forced cohabitation.

Interactions between individuals can be evaluated by recording the behavioral transitions of birds kept in the same cage. Each bird must be identifiable, for instance by color rings or wing-tags, and the observer should first create a list of behavioral categories that are displayed when the birds interact. Once this is done, the observation sessions can start. These should be carried out for a sufficiently long period (e.g., one to two hours), and distributed temporally in such a way as to cover the entire activity period of the birds over a few days. Csermely and Agostini (1993) investigated a group of rehabilitated Barn Owls by initially recording the social-agonistic interactions within the already acquainted group and then by observing possible modifications due to the introduction of a strange conspecific. The authors recorded the identity of the interacting birds and the behavior patterns of both the initiator and the follower.

The data were then transposed into a sociometric matrix to analyze both the interacting birds and the behavioral transitions. The first matrix allowed the researchers to rank the birds by aggression frequency (Table 2), leading them to compile a "social" hierarchy, while the second matrix allowed them to ascertain the probability that a certain action causes a certain type of response (Table 1). This later allowed the researchers to describe the probability that a certain pattern displayed by the initiating bird would cause a certain reaction (Fig. 2).

Table 2. A hypothetical example of a sociometric matrix used to rank individuals by interaction frequency, usually agonistic behavior. The initiating bird's identity is listed in the column on the left and those of recipient birds in the heading across the top. In this example, bird C initiated seven interactions with bird A. Bird B is the most frequent initiator (total frequency = 21), bird A is the most frequent receiver (total frequency = 19), bird F was not involved in any interactions. The data can be used to establish a social hierarchy among the six individuals.

	RECIPIENT						
INITIATIOR	A	B	C	D	E	F	TOTAL
A	——	5	2	0	0	0	7
B	9	——	12	0	0	0	21
C	7	3	——	1	2	0	13
D	3	0	4	——	3	0	10
E	0	0	0	1	——	0	1
F	0	0	0	0	0	——	0
TOTAL	**19**	**8**	**18**	**2**	**5**	**0**	**52**

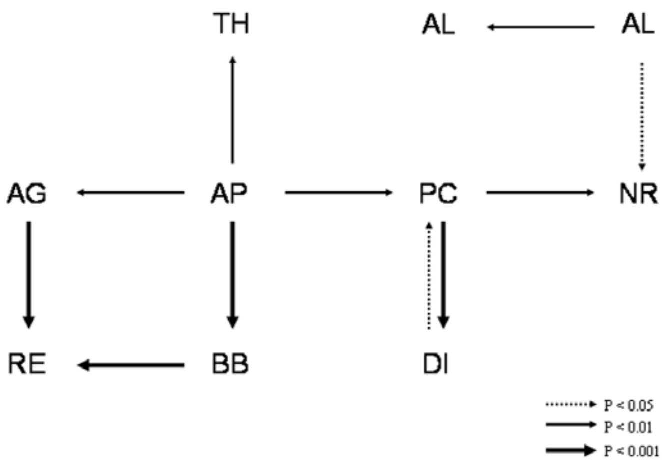

Figure 2. An example of results of a study in which behavioral sequences between individuals were assessed. The probability that any behavior displayed by the initiating bird causes reaction in the follower can be ascertained with statistical analysis and summarized graphically with a diagram similar to a flow chart. The arrows (including thickness and solid versus dashed) show the direction and probability of each sequence occurrence (AG, aggression; AL, allopreening; AP, approach; BB, bill–bill interaction; DI, displacement; NR, no reaction; PC, physical contact; RE, retreat; TH, threatening [from Csermely and Agostini 1993]).

Territorial Behavior

Territorial behavior is usually studied by observing a focal bird and recording its behavior against an intruder (agonistic display or physical aggression). Obviously, it is necessary to recognize the individuals. When radio-transmitters are used, it is important to note that radio-tracking alone is not sufficient, as it can only provide information on movements and home-range size. A detailed analysis of territorial behavior requires direct observation. Newton and Marquiss (1991) trapped and removed female and male Eurasian Sparrowhawks from their territories to verify whether their possible replacement could be attributed to movement of resident non-breeders or of neighboring individuals. In order for the researchers to answer this question, birds were banded and monitored in every territory in the surrounding area. This way, the authors verified that non-breeders of both sexes were likely present in the population and that spacing behavior was involved in limiting breeding density.

Assessing agonistic interactions in captivity can be easily performed by direct visual observation, or video recording from a blind. Preliminary observations are necessary to identify the repertoire of behaviors displayed during interactions. Observation sessions, carried out at different times of the day, provide the frequency and identity of interacting birds as well as the patterns performed by attacking and receiving birds. It also is advisable to distinguish observations carried out in the presence or absence of food, as food, being a resource to be defended, could likely be an important source of aggression.

As discussed above, the data are transposed into a sociometric matrix to assess the interacting bird dyads that are more frequent than expected, and the significant behavioral transitions. In the first instance one can obtain a social hierarchy by calculating the dominance index of each bird (Crook and Butterfield 1970) to establish a more or less linear hierarchy. In the second instance one can produce a diagram similar to a flow-chart that describes the probability that a pattern displayed by the initiating bird causes a reactive pattern in the receiving bird (Fig. 2).

Csermely and Brocchieri (1990) studied the interactions among captive Common Buzzards (*Buteo buteo*) after rehabilitation, identifying 12 social-agonistic behavior patterns and three types of vocalization. The most frequent behavior patterns recorded for the initiating bird were related to agonistic interactions, such as threatening, leg-strike, run-toward, piracy, whereas the attacked or retreating bird reacted principally performing retreat or run-toward. When food was present in the pen, piracy and run-toward were used more frequently far from the food source, whereas griffon-posture was observed most often over it.

Predatory Behavior

The study of hunting behavior in the wild often is exacting, as it is difficult to follow hunting birds. Consequently, many studies assess hunting behavior indirectly from prey deliveries to the nest or from prey remains in the nest or beneath perches. Nevertheless, only direct observations can provide information about foraging behavior, such as the rate of successful hunts, usually calculated as the proportion of successes over capture attempts.

Jenkins (2000) studied the relationship between hunting success and nesting habitat in 16 pairs of African Peregrine Falcons (*F. p. minor*). After splitting hunting behavior into several categories, he observed both partners of each pair using focal-animal sampling. He recorded hunting attempts, hunting mode (perch hunt or strikes made from air) and types of prey captured. Observation periods were classified according to season (breeding or non-breeding) and time of day. Jenkins concluded that the height of nest cliffs affected foraging success.

Cresswell et al. (2003) tested whether free-ranging Eurasian Sparrowhawks preferentially attacked vigilant or non-vigilant (i.e., feeding) prey models presented in pairs, using two types of models: a stuffed 3-week old Red Junglefowl (domestic chicken, *Gallus gallus*) and a resin-cast model of an adult European Greenfinch (*Carduelis chloris*). Half of the models of each type were mounted in a head-up position to mimic a scanning wild bird, and half were mounted in a head-down position to mimic a feeding bird. Models were placed on flexible wires planted in the ground in low vegetation. Each pair of models was connected to a camera trap. The resulting photos recorded which model was hit, and from which direction the attack occurred.

Predation also can be studied in captivity. Doing so allows the researcher to control variables and to observe behavior much more closely than in the field. Captive studies allow the researcher to investigate hunting and capture techniques, prey recognition, different responses to stimuli coming from different prey types, and maturation and refinement of the behavior sequence in the case of captive-bred birds.

To study predation behavior in captivity, it is best to have individually penned birds so as to avoid competitive interactions. The pen should be large enough, relative to the body size of the study species, to allow as natural an attack as possible. It also is advisable to equip the pen with a limited number of perches (one perch located at one end of the pen works best) so that the predation attempt begins from a fixed starting point. The prey item is placed in a small pen or enclosure opposite the perch, either on the ground or on a tabletop. The pen should be designed to prevent the prey from escaping in case the bird of prey does not attack immediately. The front should be transparent so that the predator can follow the prey's movements, but at the same time marked in some manner (painted stripes, etc.) to ensure that the bird is aware of its presence and height.

A blind, possibly equipped with a one-way window, should be placed as close as possible to the aviary, preferably immediately behind the prey enclosure, so that the researcher can record the test by direct observation or video recording. Recorded behavior patterns can range from exploratory flight, preening or movement on the perch (both interpreted as conflict patterns), to the true predation-behavior sequence. Observations can

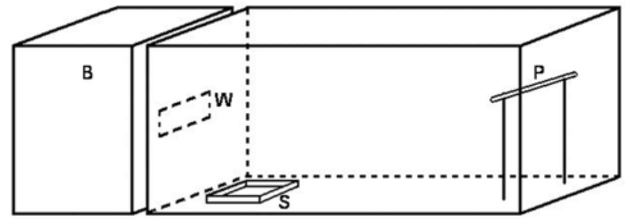

Figure 3. A diagrammatic representation of a pen for predation tests. A surface containing the prey (S) is opposite the single perch (P) upon which the bird stands. Next to the prey is a blind (B) equipped with a one-way window (W), behind which the observer records the behavior of both predator and prey.

involve the description of the attack glide, the type of landing (directly on the prey or next to it), the capture "tool" (beak, talons or both), which part of the body is grasped, and the prey's attempts to escape. Detailed descriptions of pens and recorded behavioral events are found in Csermely et al. (1989, 1991; Fig. 3).

Behavioral descriptions should be paired with temporal measurements, such as the latency from the start of the test, the frequency of each behavior and, sometimes, as in the case of preening, cumulative duration. After a successful attempt, the time elapsed until ingestion should be measured (considered latency to ingestion), and how and where in the pen it is performed are other important behaviors to be recorded. These behaviors can be recorded using check-sheets and stopwatches during both direct observation and videotape playing. An event recorder also is useful, as it automatically tracks frequency, duration, and latency of behavior.

The ethical issue of using live prey in such studies should be kept in mind and appropriate permissions sought. Captive birds of prey are easily trained to feed and to prey on dead items (Csermely 1993, Csermely and Gaibani 1998, Shifferman and Eilam 2004) and their predatory sequence is similar to that displayed when preying on live prey. Although captive studies usually are conducted to increase our knowledge of predation behavior, they also are useful in assessing the predatory abilities of rehabilitated birds. In the latter case, the use of live prey is usually necessary even from the viewpoint of the animal's well-being (cf. Csermely 2000).

BEHAVIOR AND CONSERVATION

Several authors (e.g., Caro 1998, Gosling and Sutherland 2000) have pointed out the need for ethology in conservation biology in order to ensure successful management strategies. In particular, Gosling and Sutherland (2000) state that, *"studies of behavior and conservation have a great deal to offer each other. This cross-play can happen at a number of levels. For example, the high priority given to conservation helps provide a justification for theoretically based studies of behavior and this may become increasingly important to justify research spending. Studies of behavior also can provide essential new insight into intractable conservation problems. Perhaps most important, it can also be argued that an evolutionary understanding of the behavior of individuals in populations allows us to predict responses under changed conditions with greater confidence than in the case of higher-level processes."*

In order to effectively protect a bird of prey within its habitat, it is necessary to understand its nest-site and prey preferences including the behaviors associated with these preferences. To establish a protected area of adequate size, we also must know the movement behavior of the species in question, as well as factors involved in both the intra- and inter-sexual and inter-species competition for resources. Ethological studies often require large amounts of time and money, but a project failing due to bad planning is economically more disadvantageous.

Unfortunately, and in spite of several common goals, ethology and conservation management still interact in only a limited way. Too often, ethological studies do not find application within conservation, and conservation projects often are planned without sufficient thought regarding a raptor's behavior. When used with conservation in mind, behavioral analyses can help increase success in raptor management, both in the wild and in captivity. Below we list examples of why this is important.

Raptor Rehabilitation

In rehabilitation centers, veterinary care is obviously of primary concern. Even so, such care often is not sufficient to guarantee successful rehabilitation. Conditions in captivity can be extremely stressful for raptors and can slow or even prevent their rehabilitation. It is therefore important to consider the behavioral aspects of each species in order to estimate the minimal dimensions of the aviaries, the maximum density of animals inside the aviaries, which species can cohabit, how the food must be supplied, etc.

Captive Breeding and Release to the Wild

For birds of prey at high risk of extinction, wild populations can be bolstered by offspring from the successful breeding of captive populations. The study of breeding behavior both in the wild and in captivity is very important to ensure adequate environmental conditions and to adjust rearing techniques to successfully breed captive pairs. At the same time, ethological studies also can assess whether captive-bred young behave normally and are likely to be capable of survival and reproduction in the wild. When nestlings are reared by hand, imprinting, or an imprinting-like social bond, can pose serious problems, particularly in Falconiformes (cf. Jones 1981). One way to reduce or avoid this problem is by feeding orphaned nestlings using a puppet that resembles the head of an adult. Thus, nestlings do not become wrongly imprinted on humans, and so avoid any complications in future breeding behavior. The common use of hand puppets is a useful consequence of ethological studies (Gosling and Sutherland 2000). Alternatively, hand-raising young in groups allows them to imprint on one another, thereby reducing its irreversibility (D. M. Bird, unpubl. data).

Furthermore, restocking or reintroduction projects do not end with the release of individuals. On the contrary, these projects should include long-term post-release monitoring to assess their success (cf. Csermely 2000). Behavioral studies of released birds allow researchers to determine which problems are related to the new conditions and where to look for solutions.

Specifically, applied ethology can be used to teach or to condition raptors to avoid potential threats they may encounter in the wild. One example of this is the experiment that Wallace (1997) conducted on California Condors (*Gymnogyps californianus*) at the Los Angeles Zoo. Young condors reared in captivity were conditioned using electrified wires on mock power poles not to perch on power poles once released.

CONCLUSION

In summary, behavioral studies have much to offer raptor management and conservation. Although often overlooked, this important topic promises to play a relevant role in protecting birds of prey, both in captivity and in the wild.

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