Effects of different marking techniques on the fitness of avian species.

Abstract

In science it is of great importance to differentiate individuals in certain experiments on animals. There are many marking techniques for identification of these individuals, and before, scientists did not assume that these techniques would interfere with their results. However, recent studies have shown that markings may affect certain aspects of an animal's fitness. Therefore, in this literature study, I examine the possible effects different markings may have on the fitness of avian species. I found that there are some physical effects, affecting the animal's reproductive success and mortality. Many effects due to certain markings techniques may influence one another. In some of the cases, we can differentiate between effects on mortality and reproductive success, but it is difficult to specify the cause of these effects. There was also substantial impact found of different colors of markings, mainly on sexual communication and communication with competitors, thereby affecting reproductive success of birds. Findings lead to the hypothesis that colors naturally occurring on a birds plumage or soft parts is perceived as an exaggeration of an attractive trait, so therefore perceived as more attractive, unless the concerning color is present in a congener's plumage or soft parts, indicating the possibility that color preference may play its role in the evolution of species recognition. It should be acknowledged that marking techniques may indeed have effects in certain avian species, and may therefore compromise the accuracy of acquired data. To minimize physical effects, the marking should be of proper size, suitable for the species of interest. To minimize effects caused by the use of colored markings, distribution of these colors should be truly randomized.

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Introduction

In behavioral studies on animals, scientist frequently study several individuals, so identification of these individuals is necessary to differentiate the animals. Many techniques are developed for identification for a wide variety of species. In the past, these marking techniques were applied, without any indication that these applications might interfere with data recovered from the experiments performed. Today, however, scientists discovered several possible effects these marking techniques might have on test subjects.

In 2012 I investigated the long-term effect of elevated prenatal yolk testosterone in Rock pigeons (Columba livia), to see if an elevated level of yolk testosterone would affect aggressive and courtship behavior. Here we injected pigeon eggs with testosterone (Oldenhof & Piek, 2012). We found that an elevated level of yolk testosterone leads to a decrease in courtship behavior in males, but no differences were found in aggressive behavior between the control and testosterone groups. To identify the different individuals in this study, the animals were marked with 4 rings: a number on the top left leg and a color on the bottom left, and two colors on the right leg. Colors used were neon pink, green or orange. Furthermore, the pigeons had markings on their wings, either a blue cross, a green circle or a black stripe, so that they were easy to find in the large colony. When we plotted the behavior of birds with these three different wing marks, we found a significant difference in aggressive behavior, were animals with a black stripe showed more aggressive behavior as opposed to the blue cross or green circle marked individuals. Our hypothesis for these findings, was that because Rock Pigeons have black stripes on their wings, an extra stripe may increase social status. As seen in Black headed Gulls (Eising et al., 2006) head coloration is a sign for reproductive maturity, thus in a way a higher social status, since they are more attractive to females. In sparrows badge development also increases social status (Strasser & Schwabl, 2004), where a darker colored badge mediates a higher position in the social hierarchy. So the extra stripe on an animal's wing may increase its social status towards other animals, treating it as higher placed in the social hierarchy. This in turn may reflect on the animal itself, because being treated as more dominant, it may become more aggressive towards other animals. This might be a good explanation for why black striped pigeons show increased aggression compared to green circle or blue cross marked pigeons.

This example indicates that experimental markings may have their effect on an animal's behavior. The next example of a well-known study in zebra finches shows how drastic these effects can be. In this study, performed in 1978, the parental behavior of 40 zebra finches was examined (Burley et al., 1982). The animals were marked with leg bands in combinations of seven different colors and their reproductive behavior and pair-bonding was monitored. What became clear within five months was that most birds with yellow or pink bands were breeding, whereas birds with light green bands were not. Even the birds with combinations, for example; red, pink and two shades of green were not breeding, suggesting an effect of the green toned bands. The five males with green bands still did not reproduce after 7 to 13 months. They exchanged the green bands with red bands in three of these five males and after exchange the three males reproduced within 11 weeks, whereas the two remaining males still did not. These findings indicate that the sexual behavior of the zebra finch may be affected by the leg band color of the potential partner (or possibly, by its own leg band color), as was hypothesized for aggression in the study on Rock pigeons mentioned above.

Except for this example above and my own findings, several other studies have shown that marks may have an effect on several parameters, such as reproductive behavior, aggression, migration and more. Since these effects are found in several studies they may therefore have influenced the accuracy of the results found in other studies where marks are used to identify individuals. I therefore want to examine in the next few chapter how artificial marks may affect the fitness of birds. And what could scientist do to minimize these effects? And finally, what is the biological and evolutionary implication of these findings?

First we will look at the different marks used in experiments on birds today. Then we will evaluate the effects found of these markings in reproductive success, communication towards potential partners, communication towards competitors and effects on physical or motor competences.

Marking techniques in science today

Several marking techniques are known to identify individuals in experiments. Some of these methods have been developed many years ago, but are still used in experiments today, since they have shown to be useful and are therefore hardly modified. Following is a list of common marking techniques, used in avian studies.

Wing marks

There are two types of wing marks of interest; the wrap around wing tag, and the more invasive patagial tag.

Patagial tags are a commonly used method for marking birds. They usually have a high duration and a good visibility. Tag loss is usually low in the first year, but gradually increases in later years (Patterson 1978). The tags are available in several different sizes and may consist of plastic, nylon or a vinyl fabric. Also cattle ear tags are sometimes used in investigation (Martin et al., 2010). The tags are marked with a number, or in some cases a color, to identify individuals. The patagial tag is placed on the leading part, or patagium of the wing and is visible when the bird is in flight and when the wings are in retracted position (Figure 1). The tag is secured with a stainless steel, metal or nylon pin piercing the patagium (Southern & Southern, 1985; Brua, 1998). The size of the patagial marks depend on the size of the species of interest. They should be that large that they are visible for observational purposes, yet not so large that they might hinder flight. Also, since the use of patagium tags is an invasive procedure, it should be taken into account that the animal may suffer physical damage. Also there are some reports about possible effects on behavior (see below).

Figure 1. The patagial tag. a: Placement of the patagial tag. b: Location of pin piercing the patagium. c: Example of good visibility when a bird is in flight. (Brua, 1998 (a); Smallwood & Natale, 1998 (b); maquiaambiental.com (c))

Wrap-around wing tags are similar to the patagial tags, consisting of the same material and having the same sizes. The most important difference is that the patagium is not pierced. Instead, the tag is wrapped around the patagium around the radius and ulna (Figure 2). The narrowest part of the tag can be passed between two secondary feathers, before being secured (Trefry et al., 2012).

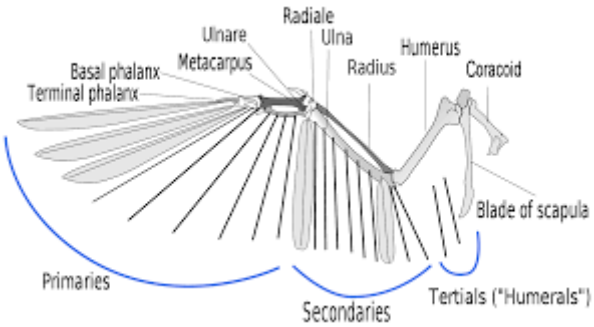

Figure 2. The anatomy of an avian wing. (blenderartists.org)

The tags can be secured by aluminum eyelets or staples (Southern & Southern, 1985). Another design is seen in the figure below, where the model of the tags enables it to secure itself by rolling up the tag ends and passing it trough the slit of the opposite tag end (Trefry et al., 2012).

Figure 3. A new patagial tag, designed by Trefry et al.. (Trefry et al., 2012)

Bill marks

Bills can be marked by nasal discs or saddles. A **nasal disc** may consist of hard or flexible plastic or nylon and is placed on one side of the bill and then connected through the nares with a nylon or metal pin (Figure 4a). Negative consequences with this method of marking is that vegetation can accumulate in this disc and there is a risk of getting the disc caught. Another method for marking the animals bill is a **nasal saddle**. Here a saddle is placed over the bill and is connected with a pin trough the nares, just as the nasal disc is, forming a patch on the animal's beak (Figure 4b-c). If the saddle is well-fitted the hazards found in nasal discs is minimized (Silvy et al., 2012). With good optical equipment the brightly colored nasal saddles are visible from distances over 400 meters (Lokemoen & Sharp, 1985).

Figure 4. a: A nasal disc. b: A nasal saddle. c: Examples of different nasal saddles. (alducks.com (a); pt-ducks.com (b); Lokemoen & Sharp, 1985 (c))

Leg bands

The use of leg bands is a widely used technique in marking birds. There are several types of these bands, starting with the bands with digits, thus a code embedded in them. These are used for identification after trapping the animal and are suitable for marking the animal for a longer period of time, but the digits might be too small to read from afar. These bands come in different sizes, depending on the size of the animal. Among these there are three types of bands; the standard butt-end band, the lock-on band and the rivet band. The most common band, the **butt-end band** is a round band with two edges that butt evenly together when closed correctly (Figure 5a). The lock-on and rivet bands are designed for raptors that are able to open butt-end bands with their stronger bill, such as hawks or owls (Silvy et al., 2012). The **lock-on band** is like a butt-end band, but has two metal rims that slide over each other and locking it in place (Figure 5b). This type of band is made from a soft metal, such as aluminum, and is removable by the bander, but not the bird itself. Finally, the **rivet band** is designed for eagles, which are able to remove even the lock-on bands (Figure 5c). Therefore the rivet band is made of a stronger metal. The rivet band is similar to the lock-on band but is secured by a rivet, or

stud locking the rims (www.pwrc.usgs.gov). For rapid identification from afar, **colored bands** are more suitable (Figure 5d). Using a set of different colors gives possibility to many combinations, since you can place multiple rings on the animal's legs and place them on the upper as well as the lower leg. Color bands are usually made of plastic and come in a wide variety of colors. The down-side of this method is that from afar, less bright colors might be less visible in some cases. Also, this method is less suitable for marking waterfowl, since their legs are not always visible. Sometimes, especially in shorebirds, colored leg bands are combined with a **flag band**; a leg band with tags extended away from the leg. (www.pwrc.usgs.gov) Leg bands should fit properly, because when too loose, the bands may get lost, leading to a biased result in survival, or the animal may be caught in its band, and when too tight, the animals leg might be constricted.

Figure 5. a: Butt-end bands. b: Lock-on bands. c: Rivet band. d: color bands. (cutlersupply.com (a); pwrc.usgs.gov (b); Ben Wurst, conservewildlifenj.org (c); K. Whittaker, courses.washington.edu (d))

Nape tags

Another technique, especially useful for marking ducklings, are **nape tags**, where a safety pin with colored plastic or vinyl flags attached to it pierces the skin of the neck. Nape tags were developed over 50 years ago (Gullion 1951, Foley 1956) but are used infrequently. Gullion also found that the nickel-plated brass safety pins can cause an acute tissue reaction. Arnold et al. (2011) developed a new type of nape tag, a smaller model than designed before with a brass safety pin with colored beads. The pins were inserted through 1 cm of loose skin directly below the base of the skull. These however were difficult to see from a distance over 20 meters, so Anderson modified the design for the nape tag by using larger color markers, consisting of either Perler beads (Figure 6a) or modified shorebird color bands (Figure 6b). With this modification, Anderson was able to identify ducklings from a distance up to 150 meters.

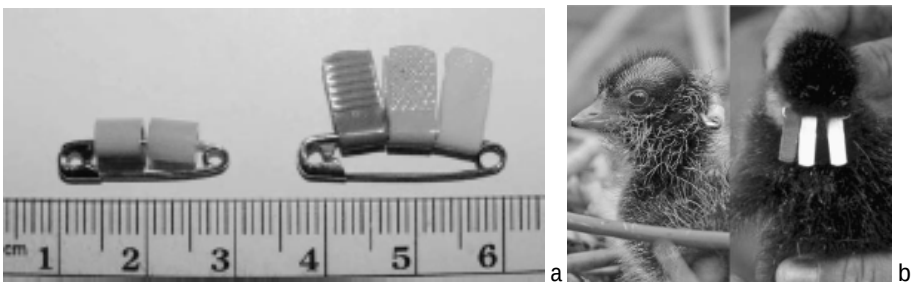

Figure 6. a: Nape tag designs: left; pin size 00 with two plastic Perler beads, right; pin size 0 with three plastic colour band tabs. b: Examples of proper tag placement on an American coot chick (left) and white-winged scoter duckling (right). (Arnold et al., 2011)

The examples above may suggest that some of these methods may affect the animal physically, perhaps even injure it. Other than physical consequences, particular markings may affect certain behavior, because many bird species are visually stimulated by certain colors or ornaments. In the next chapter I will discuss a number of studies, where possible effects of marking methods are evaluated.

Physical effects

First, we will look at the physical effects of certain markings on the reproductive success and mortality.

Rerproductive success

There are several reports on effects of patagial tags on reproductive success. However, it is difficult to assign these effects to a specific cause. For instance, patagial tags are associated with lower reproductive performance in common eiders (Bustnes & Erikstad, 1990). In this study a colony of common eiders was observed and Bustnes & Erikstad found that tagged hens layed six days later than other animals did. Clutch size was similar among the different groups, but tagged hens laid smaller eggs. Because common eiders depend heavily on stored body reserves for breeding, inability of gaining mass could explain these differences in reproductive success in common eiders. Bartelt & Rusch (1980) found some effects of markings on the body weight of American coots. An effect was found on body weight in adult coots, but a greater effect was seen on the body weight of juveniles, with neck bands having a smaller effect than patagial tags did. With neck bands adult and juvenile coots gained weight, with a mean daily weight change of 1,8 and 3,1 g/day respectively, whereas with patagial tags adults and juveniles lost weight with a mean weight change of 1,9 and 4,4 g/day respectively (Bartelt & Rusch, 1980). With patagial tags the animals had a lower body weight than usual, possibly due to lessened foraging efficiency. This effect is probably similar to the situation in the study of Bustnes & Erikstad (1990). In the study of Southern & Southern (1985) on ring-billed gulls, no effect was found on brood size, but in a previous study there was. Here was found that wing-tagging resulted in a smaller brood size, as opposed to adjacent untagged birds (Southern & Southern, 1983). Sample sizes were larger in the previous study, so possible impacts of patagial tags on reproduction should be acknowledged.

Other studies, however, did not report such effects. For example, no effect was found on the reproductive success or breeding activities in golden eagles (Phillips et al., 1991). In least terns, there was no effect of several different marking techniques, while capturing techniques did have their effect though. Capture by cannon nets at loafing areas showed no effect, but terns that were nest-trapped deserted the nest at greater rate than other birds did (Brubeck et al., 1981). In American kestrels no effect was found on reproductive performance, nor was there any effect found on their flying abilities, foraging abilities or social behaviour. It should be noted that a new kind of patagial tag was used here, optimized for the size of the bird (Smallwood & Natale, 1998). As noted before, the size of the tag should be chosen with care, so that the animal does not experience hindrance.

What also influences reproductive success is mating success, where communication with potential mates plays a great part. This sexual communication may also be affected by patagial tags. In ring-billed gulls, most tagged females (54-60%) were unable to acquire males as a partner and they were rejected more often (Kinkel, 1989). Also birds that changed mates tended to avoid a tagged bird as a new mate. Tagged males did not experience more rejection. Possibly the male gulls were aware of this physical difference (the tag itself). Another explanation is that tagged females showed submissive behaviour, unattractive to males. Tagged females were very subordinate, and often in sleeked-upright posture, however, quantitative data for this hypothesis is missing (Kinkel, 1989).

Mortality

Coots marked with neck bands or patagial tags showed signs of confusion immediately after being marked. The coots bit the marker or dragged the marked wing as if it was injured (Bartelt & Rusch, 1980). In some cases marked animals were preening their mark. This was seen in wing-tagged ring-billed gulls (Southern & Southern, 1983) and common eiders (Bustnes & Erikstad, 1990), and in ruddy ducks, marked with a nasal saddle (Koob, 1981). Here, marked animals spent more time in maintenance than other, unmarked animals did and even spent less time in loco motor activities and in finding a mate. In other avian species that ruddy ducks or other small species, the nasal saddle has shown no effect on the animal's behavior, especially when medium to large-sized. This might be due to the fact that the nasal saddle is quite big in comparison to the animal's bill, as in the

ruddy duck. The ruddy duck has relatively small nares and the bill consists of a fleshy tissue, what may be the reason for irritation from the saddle (Koob, 1981).

Another issue is the possibility of injuries due to the use of certain markings. Indeed, there are some reports on skin and feather abrasion in prairie falcons (Kochert et al., 1983), herring gulls (Mudge & Fern 1978) and ring-billed gulls (Southern 1971) where they used patagial tags for identification of individuals. In dabbling ducks, there was damage found to the nares of the bill after using nasal saddles. When a larger nylon nasal saddle was used, more vegetation was gathered in some cases, hereby damaging the culmen above the nares of the bill. Regular sized saddles showed no such effect (Lokemoen & Sharp, 1985). Using leg bands also showed cases of injuries. There is seen scraping of the skin of the leg (Reed, 1953) and even leg amputation when constricted (Atherton et al., 1982).

Also, mortality due to the tags is possibly increased in American Kestrels (Bolen & Dreden 1980) and willets (Howe 1980). And as mentioned earlier, in ring-billed gulls, significantly fewer animals marked with patagial tags returned to the colony site as opposed to color-banded birds (Kinkel, 1989). In the Australian white ibis, patagial tagging with cattle tags had no effect on the animal's health, at least in adults. But some of the nestlings died due to marking with the patagial tag, especially those with relatively low body weight. So for these younger, smaller animals, another marking method, like color banding, should be used (Martin & Major, 2010). Another option for marking birds is using neck bands. For this method, it should be considered that the proper size is used, to prevent constriction or worse; in coots, there were several cases in which the lower jaw of the bird was seen caught in the neck band in one case even leading to death of the animal (Bartelt & Rusch, 1980).

A new method using nape tags, as discussed in the previous chapter, was applied in American coot chicks (Figure 6). Occasionally a chick got its bill caught in the tag, but was always able to free itself quite fast. Other than that no harmful effects were found and this could be a good technique of marking other species, like hatchling loons, grebes, goslings and gallinaceous birds (Arnold et al., 2011).

The examples above show that patagial tags may injure the animal, so when the animal's wing is injured, it is likely to assume that flight is impaired. And indeed, in a study of Kinkel (1980), an effect was found on migration. In comparison to color-banded birds, fewer tagged birds returned to the colony-site, possibly due to a higher mortality. Among the tagged birds, more males were spotted on return than females (Kinkel, 1989). Tagged birds arrived one week later at the colony-site than the banded birds did and all the tagged birds bred 2-5 days later than color-banded birds. This was not explained by the fact that the birds arrived later at the colony-site (Kinkel, 1989). The same observation was made in another study in wing-tagged ring-billed gulls, where a significantly lower proportion of the patagial-tagged birds returned to the colony site than color-banded birds the year after marking. A possible explanation could be that birds moved to different colony sites, but this was extremely rare; 3 times in the five years before this study (Southern & Southern, 1985). A more plausible explanation would be that there was an interference with migration due to the patagial tags, as Howe (1980) showed in willets. He found that willets were unable to finish their round-trip migration due to wing tags, where none of the wing-marked birds returned, because of hinder in flight, probably due to increased drag or abnormal feather displacement (Howe, 1980). This interference in migration is supported by the fact that ring-billed gulls that did return to the colony site, returned six days later than color-banded birds did (Southern & southern, 1985).

It is clear that many effects due to certain markings techniques may influence one another. In some of these examples discussed, we can differentiate between effects on mortality and reproductive success, but it is difficult to specify the cause of these effects. For example, patagial tags in ring-billed gulls may affect migration, because of hinder in flight. In turn, hinder in flight may lead to less efficiency in foraging abilities, which may lead to higher mortality or reduced breeding ability. This will be discussed later on in the conclusion. Beside the

effects that the physical form of he markings may have on an animal's fitness, the color of the markings used may have certain influences as well. In the next chapter I will discuss these possible influences.

Effects of colors

Many avian species depend on visual stimuli in communication, so colors may play a great part in this communication, as was mentioned in the introduction. Again, we will look at the effects found on reproductive success and mortality, this time due to different colors of the markings, mainly colored leg bands.

Reproductive success

With respect to reproductive success, two aspects in reproduction will be discussed: communication in partner finding and communication with competitors, because these two aspects can influence the reproductive success of an individual.

Sexual communication

Colored leg bands may have their influence on communication, often depending on the color of the band. In zebra finches, for example, the females beak is colored orange, whereas the males beak is red. Juveniles resemble females in appearance, with the exception that their beak is colored black. And indeed, experiments by Burley (1982) showed that male zebra finches preferred females with black, bright-pink and red bands and avoided those marked with light-blue bands, and females preferred males with red bands and avoided those with light-green bands (Figure 7; Burley et al., 1982). Attractiveness was measured as the time test subjects spent associating with stimulus birds banded with one of several colors in relation to the time spent with unbanded birds.

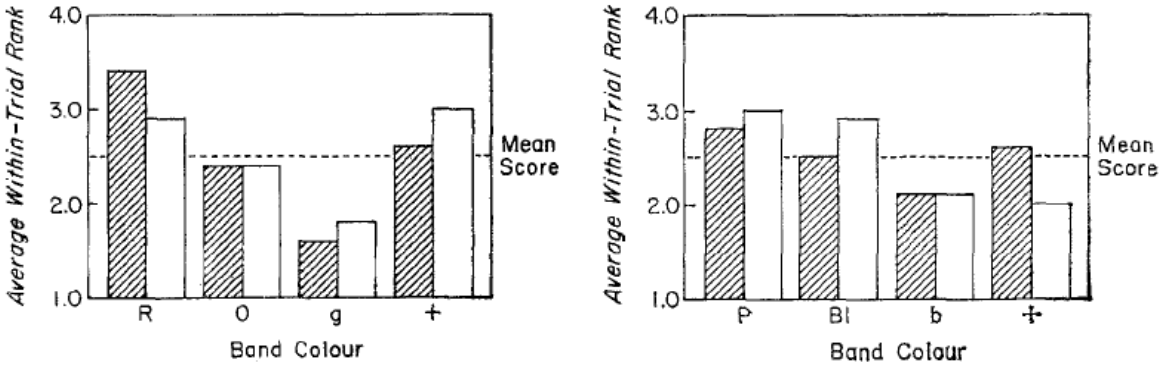

Figure 7. Responses of zebra finches to different band colors. Preferences were observed, by measuring time spent by animals on the same perche as the stimulus bird, marked with the colors of interest. Within trials results are ranked 1-4, where 1 represents the band color with which the subject spend the least time. Averages for all trials are shown. Female responses indicated by hatched bars; male responses by open bars. Left: red (R), orange (O), light-green (g) and bandless (+). Number of subjects: females = 11; males = 13. Number of trials: females = 38; males = 45. Right: bright-pink (P), black (Bl), light-blue (b) and bandless (+). Number of subjects: females = 6; males = 7. Number of trials: females = 36; males = 36. (Burley et al., 1982)

Female zebra finches preferred the color red; the color of the male's beak. Male preference was found for the colors black (present in the female's plumage), pink and red (resembling the color of the female's beak) (Figure 8a). Burley proposed that band color preferences tend to correspond to colors naturally occurring on the species (Burley, 1986a, Burley et al., 1982). This hypothesis is supported by a study in band color preferences in female double-bar finches, closely related to zebra finches (Burley, 1986a). As opposed to the zebra finch, which has a black, orange or red beak, double-bar fiches have a greyish-blue beak (Figure 8a-b). Preferences of double-bar finches and zebra finches were tested for the colors bright-red, light-blue and bandless (Figure 9;

Burley, 1986a). Indeed, double-bar finches preferred light-blue banded birds over bandless or red-banded birds, even in isosexual selection (social interactions with the same sex), whereas the zebra finches preferred the red-banded birds.

Figure 8. a: A zebra finch pair (right: female; left: male) b: Double-bar finches c: An American goldfinch (Max Planck Institute for Ornithology (a); Bill van Patten, fabulousfinch.com (b); Journal of Consumer Research (c))

Female American goldfinches also show a preference for the band color orange, the color of the males beak (Figure 8c) (Johnson et al., 1993). These findings support the hypothesis of band color preferences corresponding to the colors naturally occurring on the species.

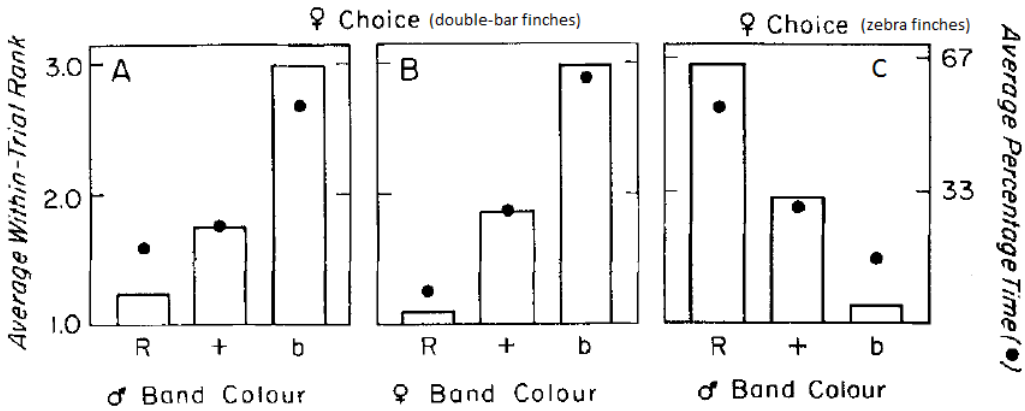

Figure 9. Band color preferences for the colors bright-red (R), bandless (+) and light-blue (b) . a: Heterosexual preferences of female double-bar fiches. b: isosexual preferences of female double-bar finches. c: Heterosexual preferences of female zebra finches. (Burley, 1986a)

In Red-cockaded woodpeckers, red leg bands are seen as less attractive by females, and can reduce male fledging success and can affect sex ratios in offspring (Hagan & Reed, 1988). In male Red-cockaded woodpeckers, the only red features are the cockades, small tufts of red feathers just above and behind the eyes, usually only visible when the bird is disturbed (Figure 10).


a

b

Figure 10. a: A red-cockaded woodpecker. b: The red cockades on a male red-cockaded woodpecker. (Joe Kegley, wildlifesouth.com (a); Carlton Ward Jr., magazine.nature.org (b))

The reason that these red bands are found unattractive, might be that red functions as a signal of aggression, which, in case of the leg bands, cannot be concealed. This constant agitated state can be less attractive to females, signalling for reduced parental care (Hagan & Reed, 1988). They also found that males with red bands produced fewer male offspring than males without red bands. This finding was consistent with the findings of Burley (1985). She found that the offspring sex ratios tend to be biased towards the parent with the most attractive features in zebra finches. Birds with "attractive" leg bands also produced more young than the other birds did (Burley, 1986b). Females might invest less time in parental care in male offspring when mated to an unattractive mate (Hagan & Reed, 1988) and this is consistent with the differential-allocation hypothesis. This states that an individual's own attractiveness affects the amount of parental care their mate is willing to invest in their offspring in species with biparental care. Individuals are willing to provide above average parental investment when the chance of maintaining relative attractiveness is present, so less attractive individuals must accept mates investing less (Burley, 1986b).

A specific color leg band may also be seen as an exaggeration of an animal's ornament, often involved in sexual selection. In rock ptarmigan (Figure 11), the size of their supraorbital red comb is a measure for a male's competitive ability; the size reflects a male's aggressiveness and the condition of the combs reflects whether or not the male has success as a fighter. In wild rock ptarmigan red colored leg bands on males are more attractive to females, possibly signalling for higher competitive ability (Brodsky, 1988). So this contrasts with the findings in the red-cockaded woodpecker (Hagan & Reed, 1988).

Figure 11. A Rock ptarmigan (Arthur Morris, birdsasart.com)

In my own study (Oldenhof & Piek, 2012) I found that male rock pigeons marked with a black stripe showed significantly more aggressive behavior towards other animals than birds marked with a green circle or blue cross. Our hypothesis for this finding, was that individuals marked with black stripe were treated as more dominant, therefore behaving more dominant towards the other birds. This would be consistent with the findings in Burley's studies on zebra finches (1982; 1986a), where she hypothesized that an exaggeration of an individuals trait, as plumage color, makes an individual more attractive and as a result more dominant. Since

Rock pigeons have black stripes on their wings (Figure 12), this extra stripe may be seen as this exaggeration. Another explanation, however, might be that the animals marked with a blue cross or green circle were seen as more submissive, therefore undergoing more aggressive behavior from their black-marked neighbors. Since the focus of our study lied on the aggressive and courtship behavior as a result of yolk-injected testosterone, rather than influences of different markings on this behavior, data for this hypothesis is missing.

Figure 12. A Rock pigeon (Lyn Topinka, northwestbirding.com)

Though there are effects found of colored leg bands in the examples above, colored bands do not affect ring-billed gulls. As told in the previous chapter, patagial wing-tagged females were rejected in 60% of the times by male birds (Kinkel, 1989), but no such effect was found among the different colors leg bands, nor in leg bands opposed to unmarked birds. Apparently, leg color is not important to this species in courtship activities (Kinkel, 1989).

Communication with competitors

As mentioned in the previous paragraph, the red cockades in male red-cockaded woodpeckers are signal for aggression. Because the red-colored leg bands can be seen as a constant sign for aggression, they hereby might incite more group aggression, because of their inability to express submissiveness (Hagan & Reed, 1988). This effect is also demonstrated in red-winged blackbirds (Figure 12). Male blackbirds have red epaulets, patches of red colored feathers on their wings which they can hide and fully expose during territorial and sexual displays. In a study of Metz & Weatherhead (1991), males with red leg bands experienced more aggression from his neighbors. This due to the fact that the males could not conceal their red-colored bands, as they can with their epaulets and therefore signal aggressiveness when trespassing another birds territory. This effect may be strengthened by the fact that birds are aware of the competitive ability of their neighbor. Animals living closely to each other, can observe their neighbors competitive interactions and so competitive abilities. So when an animal with red bands shows aggressive signaling that is inconsistent with its competitive abilities, seen by its neighbor, the neighbor may be aware of the signal being false. As a results the red-banded individual may be challenged more by its neighbors, because it constantly displays aggression (Metz & Weatherhead, 1991). In another study of Metz & Weatherhead (1993), where they used a model bird with either black, blue or red leg bands, that was placed outside of another animal's territory, the animals were most hesitant to attack the model with the red leg bands, opposed to the models with the black or blue bands. Birds spent more time further than 10 meters away from and showed lower intensity of song display around the red-banded model (Metz & Weatherhead, 1993).

Figure 12. A red-winged blackbird (Greg Forcey, umesc.usgs.gov)

In zebra finches, red bands on males are seen as more attractive to females and green bands as less attractive. Cuthill et al. (1997) examined whether these colors might have an effect on not only male-female interactions, but in male-male interactions as well. Here they studied the dominance of male zebra finches by measuring time spent by a single feeder, accessible to four different birds. They scored the number of times an individual displaced another bird from the feeder, thus being more dominant, or being displaced from the feeder, thus being subordinate. The red-banded birds were often the displacer and were rarely displaced, whereas the green-banded birds were frequently displaced and were rarely the displacer. So this suggest that the red banded birds were more dominant and the green-banded birds more subordinate. The same effects were found when red or green birds were put together with un banded birds, suggesting that both effects may operate, namely that red bands result in more dominant behavior and green bands result in more submissive behavior. The fact that direct aggression was not affected by color bands, suggest that the red bands intimidate another bird, rather than enhancing the aggressiveness of the wearer (Cuthill et al., 1997).

In the study of Cuthill et al. (1997), animals with green, less attractive bands were inhibited in their access to food. One may think that this will affects the animal's health, not being able to feed properly, so possibly this effect on dominant and subordinate behavior may result in an effect on health an therefore mortality.

Mortality

In zebra finches in breeding populations, males with red bands had a longer life span than the males with orange or light-green bands, as had females with black bands, which lived longer than females with orange or light-blue bands (Burley, 1985), where animals banded with less attractive colors had a higher mortality than unbanded birds. Here the specific cause of death was not determined, but it was clear that the animals died from a variety of specific causes. Animals showed premortum declines in physical condition, including declined feather condition, weight loss, changes in beak color, loss of balance and adoption of postures typical for ill birds (Burley, 1985).

Other than these findings above, I found no effects on mortality in birds due to colors of certain markings.

Conclusion

Patagial tags mainly have their influence on physical aspects, which in turn translate to migrational and reproductive success and even mortality, whereas colored leg bands have their effect mainly on communication aspects, as communication in partner finding or communication with competitors. First, we will discuss the findings on physical effects.

The physical effects found on avian species, caused by several marking techniques may influence several aspects of an animal's fitness. I found that it affects reproductive success, mortality and migration due to certain injuries. Injuries or excessive drag may hinder flight, which in turn may affect migration, as well as mortality. Also the excessive drag, or hinder in flight, in this example due to a patagial tag, may lead to less efficiency in foraging behavior, which in turn may lead to mortality, but to declined reproductive success as well. Females depend heavily on stored energy reserves when they go into breeding, so when they are unable to forage efficiently, they are unable to breed. So again, the primer effect can lead to negative effects on different aspects of the animals fitness. Scientist should acknowledge these possible effects and should choose the proper marking for the species used in their experiments. With the use of patagial wing-tags, the size of the tag must be adjusted to the size of the animal, so it causes as little hindrance as possible. The same protocol accounts for neck bands and nasal saddles. With nasal saddles, it should be noted that avian species with fleshy nares may get injured by this marking technique, so another marking technique might be more suitable. Increased mortality was found with patagial tagging in younger, smaller birds. A solution for this is the nape tag, developed by Arnold et al. (2011), which was shown to be suitable for marking smaller or younger birds. A final problem found in using patagial tags, is that injuries were found in several species, such as skin and feather abrasion. This shows the difficulties in marking animals, even when the tag is of proper size. The use of leg bands has shown little injuries, so this technique might seem a good solution to the problem of marking birds, other than waterfowl. However, this technique has been shown to have substantial effects on communication aspects in certain avian species.

Effects of leg bands are due to the different colors of the bands, where the influence of leg band colors on behavior appears to vary according to species, in particular whether the color matches those found on the bird's plumage or soft parts. When the band color is present in a bird's plumage or soft parts, attractiveness of this particular color varies among species. As was seen in the red-cockaded woodpeckers and red-winged blackbirds, the band color red, naturally present on the male bird's plumage, provokes aggression in other birds and is therefore found unattractive by females. On the contrary, when zebra finches and double-bar finches wore a colored leg band of the same color naturally present on the bird's soft parts, this was seen as an exaggeration of the animal's natural color and was found more attractive.

These findings of colors in communication in partner finding contradict one another; in one species an exaggeration of an individual's color is seen as more attractive while in the other species it is seen as less attractive. A mechanism explaining these differences is that an exaggerated color can be preferred unless that specific color is present in closely related species. Burley (1986) found that colors naturally occurring in congeners, were avoided by zebra finches and double-bar finches (Figure 9). This is consistent with the findings in red-cockaded woodpeckers (Hagan & Reed, 1988). Here males have less red in their plumage than other south-eastern U.S. species of woodpeckers do, and indeed, males with red leg bands, the color of their congeners, are found less attractive to females. So the exaggeration of red in red-cockaded woodpeckers resembles another species and is therefore avoided by potential partners. This might indicate the possibility that color preference may play its role in the evolution of species recognition.

These findings are important to consider, because when certain markings can influence an animal's communication, it can affect data obtained in experiments. Especially when a study is performed in reproductive success, aggression, and even mortality, these findings above show that the result can be biased dramatically when possible effects are not taken in consideration.

One may conclude that avoidance of colors present on the plumage or soft parts of congeners is sufficient to rule out a part of possible biased results due to interference in communication in avian experiments. However, this hypothesis is supported only by a small number of studies, for a small number of avian species. Further investigation is needed to confirm, or at least support the hypothesis that an animal avoids colors of leg bands found in closely related species. On the other hand, when this is in fact confirmed, it will still be very difficult in choosing the correct colors for marking your animals, since there might be several closely related species with many different colors in plumage and soft parts. Furthermore, attractive colors should be avoided as well, since these also introduce bias to results. To minimize systematic bias, the process of assigning band colors should be truly random. This means that band color should not be used in differentiating certain groups, for example sex, age class or place of origin. Another solution might be to change band colors randomly halfway trough the experiment.

The studies I cited were about effects on fitness in avian species, but these findings may apply to other species as well. Sexual dichromatism for instance, is not only present in many avian species, but also in other species, so it is likely to assume that effects colors may also arise in these species. Though minimizing these possible effects can be difficult, scientists should take into account that in some cases bias may occur due to their marking techniques, though it is probably impossible excluding effects of marking, as well as handling, of animals completely in scientific studies.

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