



Impaling in true shrikes (*Laniidae*): A behavioral and ontogenetic perspective

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Abstract

The impaling of prey is a behavioral trait restricted to the true shrikes (*Laniidae*). Here, we suggest the ontogeny of this behavior. We believe impaling originated from wedging behavior that occurs among several other groups of birds, including corvids. Accidental impaling during wedging was likely the behavioral precursor of purposeful impaling. Fidelity to impaling sites lead to the creation of caches, which were eventually used by females for male evaluation. Caching allowed males to increase their fitness by using the caches as a display to attract potential mates. Further, caching is used by shrikes to demarcate territories, store food for inclement weather or periods of stress in the breeding cycle, divide labor between the breeding pair, and for “aging” while deterrent chemicals in prey decompose.

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The role of impaling behavior in the biology of the true shrikes (*Laniidae*) has been extensively studied (e.g., Brewster, 1894; Watson, 1910; Donovan, 1929; Miller, 1937; St. Paul and Gwinner, 1967; Beven and England, 1969; Wemmer, 1969; Yosef and Pinshow, 1988; Esely and Bollinger, 2003) and other animals (e.g., Young et al., 2004). However, the evolutionary development of this unique tool is unstudied although its ontogeny in young shrikes is well known (Miller, 1931; Wemmer, 1969; Smith, 1972, 1973;

Busbee, 1976). Other taxa have behaviors similar to impaling. For example, some Australian Butcherbirds (*Craticidae* spp.; Pizzey and Knight, 1997) and African Boubou Shrikes (*Laniarius ferrugineus*; Sonnenschein and Reyer, 1984) are known to wedge prey, apparently to save handling time, however, these species never impale prey on thorns. By contrast, in the *Laniidae*, vertebrate prey is impaled on sharp objects, decapitated and, in most cases, the brain consumed before other body parts (Yosef, unpublished data).

Impaling is defined as the skewering of prey on a sharp projection; “wedging” is the placing of the item in the fork of a substrate (branch, barbed wire, etc.)

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that allows the predator to manipulate and feed on a prey item. In some cases, while the predator attempts to wedge the prey it may be accidentally impaled on a sharp projection, but intentional and systematic impaling, as it occurs in the true shrikes has not been documented in any non-Laniidae bird species. Both wedging and impaling are considered tools that facilitate dismemberment of prey at lower energetic costs to the predator (Schon, 1994; Cade, 1995).

Most studies of impaling have concentrated on the Loggerhead (*Lanius ludovicianus*), Red-backed (*L. collurio*), Woodchat (*L. senator*) and Great Grey Shrike (*L. excubitor*). Field observations confirm that the ability to impale prey develops in the young of these species in the first 4–5 weeks after fledging (Miller, 1931; Cade, 1967; Wemmer, 1969; Smith, 1973; Busbee, 1976; Yosef, unpublished data). Although Lorenz and St. Paul (1968) concluded that impaling was innate in young shrikes, they suggested that it could only be mastered by practice and experience. Busbee (1976) also considered experience an important component in the development of vertebrate predatory behavior and concluded that a definite ontogeny must occur before impaling proficiency could be achieved. These ideas are consistent with the findings of Ashmole and To-var (1968) and Recher and Recher (1969) showing that capture rate, capture efficiency, prey size and handling time improved with age in avian predators indicating that there is a learning component in avian predatory behavior.

Shrikes are similar to diurnal raptors (Falconiformes) in their predatory behavior, but in contrast they do not possess the strong talons that the larger raptors use to dismember prey (Schon, 1994; Cade, 1995; Vander Wall, 1990). It has been suggested that shrikes have overcome this limitation by evolving impaling behavior that allows them to increase the size of exploitable food items (Whyte, 1887; Olsson, 1985; Yao, 1985). Wemmer (1969) and Valera et al. (2001) found that the unpredictable and transitory nature of food surplus seemed crucial to initiate impaling behavior. Moreover, the composition of caches of impaled food was found to be a function of the distribution and accessibility of the prey (Whyte, 1887; Durango, 1956; Kobayashi, 1980; Yosef and Grubb, 1993; Tryjanowski et al., 2003).

Caches made prior to pair bonding and the start of the breeding season may be indicative to females of male quality and the potential parental ability to supply

food (Yosef and Pinshow, 1989; Sarkozi and Brooks, 2003). During the period of pre-nuptial display, male shrikes were observed to impale inedible objects such as rags, snail and eggshells, faecal sacs or even bread crusts, ostensibly to boost the visual effect of the cache (Durango, 1956; Lorenz and St. Paul, 1968; Yosef and Pinshow, 1988; Leonard, 1992). In this light, it was suggested that male quality was evaluated, not only by the visual impression of the conspicuous cache, but also by the composition of the impaled prey items; this even though caches were continuously subject to kleptoparasitism (Yosef, 1989). In addition, fitness was positively correlated to initial cache size. Not only was reproductive success higher in males with larger caches, but also polygynous breeding occurred in them more often (Yosef and Pinshow, 1988; Yosef et al., 1991).

Esely and Bollinger (2003) found a positive correlation between impaled prey abundance and the number of fledglings produced per successful nest. The facts that shrikes persist in maintaining conspicuous caches even when their young have hatched and that they impale inedible objects such as egg shells and faecal sacs under the continual threat of kleptoparasites, which may even endanger their young, have prompted several authors to suggest that this exhibitionism has a role in reducing the energetic costs of territorial defense during the most strenuous part of the birds annual life cycle (Mizzel, 1993). In fact, Mizzel (1993) and Sarkozi and Brooks (2003) hypothesized that impaling plays a role in advertisement of territory ownership and the territorial boundaries defended.

Other explanations that have been proffered to explain impaling behavior. For example, many studies on foraging have suggested that caching or hoarding, i.e., the creation of a larder for later use, is the major function of impaling (Karasawa, 1976, 1982; Carlson, 1985; Vander Wall, 1990; Severinghaus and Liang, 1995). Burton (1999) proposed that the impaling of old nest material by shrikes for later use results in inedible objects remaining impaled after the construction of a new nest is accomplished. Burton suggested that this behavior could have been the progenitor of the impaling of large prey items for dismemberment. Applegate (1977) theorized that impaling might serve to clearly divide sex-specific tasks between the parents, i.e., males hunt and impale while the females feed themselves and their young from the caches. Yosef and Whitman (1992) reported an interesting exaptation of impaling behavior.

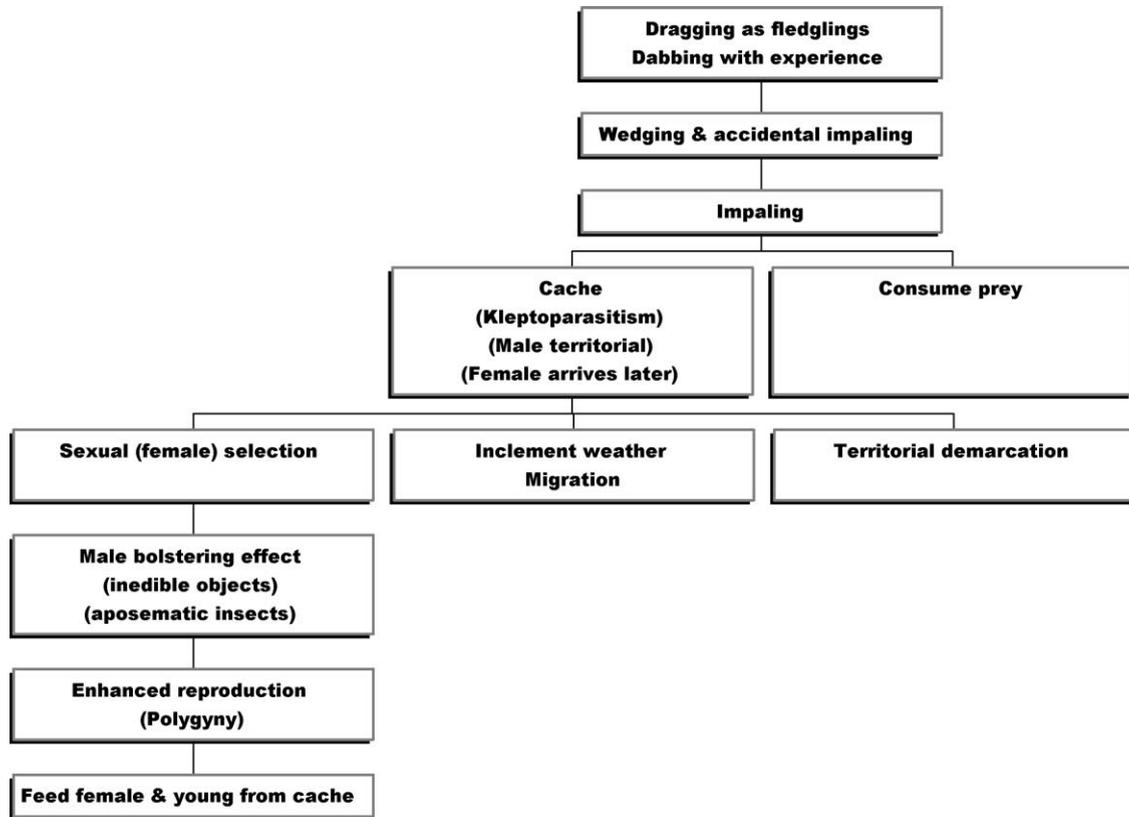


Fig. 1. Ontogeny of impaling behavior in true shrikes, *Laniidae*.

They found that aposematically colored and chemically defended lubber grasshoppers (*Romalea guttata*) were impaled by loggerhead shrikes, aged until the deterrent chemicals decomposed, and eventually consumed.

Consolidating at this juncture (Fig. 1), we posit that impaling is an innate behavioral characteristic that is refined by learning and practice. Fledgling shrikes are known to play with inedible objects while still being fed by their parents and to indulge in “dragging” behavior that later develops into what was termed “dabbing” (Smith, 1972; aka “Tupfbewegungen”; Lorenz and St. Paul, 1968). Once the fledglings are able to catch prey for themselves, they develop individual variations in their prey handling.

The sole use of impaling by fledglings is to assist in the dismemberment of prey. The young also return to impale where they successfully impaled previously, usually at places where they engaged in dabbing (Yosef, unpublished data). We think that this fidelity to impal-

ing sites has carried over into their adult behavior. If viewed in the perspective of evolutionary time, and taking into account that no other avian species has ever gone beyond the stage of dabbing or wedging (Smith, 1973), we consider the fidelity to favorite impaling sites to be the basis for the evolution of this behavioral trait which evolved from simple dabbing by fledglings, to wedging while gaining experience, and eventually to proficient impaling in adults that are now able to exploit prey that would otherwise be inaccessible.

Based on our observations in the Sede Boqer area, Israel (1986–1989), and at the MacArthur Agroecology Research Centre, in Florida (1989–1993), we consider sexual selection by females to have been a selective force behind the various exaptations of impaling that have been reported. The pattern of change in impaling behavior might have gone like this: in the past when females arrived at the breeding grounds, they evaluated the male and his territory quality by visually

identifying the locations of the cache sites and their contents. Responding to what the females were using as an index of quality, the males probably not only resorted to killing prey beyond their own needs and impaling the excess in their caches, but also to adding small prey items that could otherwise be consumed with relatively little handling cost. In order to enhance the visual impression of the cache, the males also impaled inedible, but often colorful, objects. This is probably when aposematically colored, chemically defended insects were impaled—initially as visual cues, but that after a time detoxified and became edible (Yosef and Whitman, 1992; Yosef et al., 1996; Fuisz and Yosef, 2001).

The culmination of this process is that males with the biggest caches mate with the earliest arriving females, resulting in higher than average number of nesting attempts and a subsequently large number of fledged young (Yosef and Pinshow, 1989; Evely and Bollinger, 2003), or in extreme cases resulting in polygyny with a male having two females breeding in his territory in parallel (Yosef, 1992a; Yosef et al., 1991; Lorek, 1991; Olsson, 2001; Probst, 2001).

During the courtship feeding stage, which is relatively short in comparison to other passerines, the food offered to the female by the male is invariably fresh. Later, when the female is mostly incubating or brooding the nestlings, the male can supplement the prey brought to the nest with items from his cache and replenish the cache when time is available. We have noted that male Great Grey Shrikes do not feed hatchlings until they are at least 5 days old—the nest is the exclusive domain of the female and she does all the feeding (Yosef, 1992b). Incubating or brooding females have been observed flying to and eating directly from the cache. The amount of prey in the caches drops significantly during the fledgling and post-fledging period, when the family consumes all the prey and the parents impale only for dismembering the larger prey items. The pieces are then transported to the family (Yosef, 1992b). In most of the cases, where we observed the decapitation of an impaled vertebrate, the male consumed the brain and the head, and the body was delivered to the female and the young.

To conclude, through evolutionary time the *Laniidae* have modified the behavioral adaptation of impaling from a tool to dismember into a wide range of exaptations. The behavioral adaptation that begins as dragging, then dabbing and wedging, and is then per-

fecting as impaling is unique in nature and requires further study to understand the ecological processes driving its development and diversification in the *Laniidae*. This is paper number 479 of the Mitrani Department of Desert Ecology.

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