

IS FOOT SQUEEZING PRESSURE BY TWO RAPTOR SPECIES SUFFICIENT TO SUBDUED THEIR PREY?¹

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Abstract. We quantified foot squeezing pressure exerted by Common Buzzards (*Buteo buteo*) and Eurasian Kestrels (*Falco tinnunculus*) while grasping a rodent. The birds were offered either a dead laboratory mouse, a fake mouse consisting of a laboratory mouse skin surrounding a rubber pipe connected to a pressure transducer, or a live laboratory mouse. Direct observations and necropsy of the depredated mice confirm death by suffocation from the raptor's grasp. The two raptor species differed in technique of constricting the fake mouse: the buzzard relied on strong, but very brief squeezing bouts, whereas the kestrel compensated for less squeezing strength by performing constriction with prolonged duration. When observed, bites to the head were consistent with immobilizing live prey but not killing it. In contrast, squeezing by thoracic compression is sufficient to kill the prey without the need to use beak or talons.

Key words: *Buteo buteo*, *Common Buzzard*, *Eurasian Kestrel*, *Falco tinnunculus*, *predation*, *prey killing*, *raptors*.

The techniques raptors use to kill prey have received little attention. Detailed descriptions of attacks are rare (Goslow 1971, Mueller 1974, Cade 1982) and are mainly limited to success, frequency, daytime distribution, and prey species. The Common Buzzard (*Buteo buteo*) and the Eurasian Kestrel (*Falco tinnunculus*) are opportunistic feeders, with a wide spectrum of prey ranging from small invertebrates to small rats (kestrels) and small hares (buzzards) (Cramp and Simmons 1980, Village 1990).

More recently, Csermely (1994) and Csermely et al. (1998) ascertained that Eurasian Kestrels do not use either the bill or the talons to kill mice and rats, but squeeze their prey until it suffocates. The aim of our study was to quantify the foot squeezing pressure exerted by both Common Buzzards and Eurasian Kestrels during realistic predation attempts on small rodents and to determine whether the foot pressure performed by raptors is compatible with the hypothesis of killing by thoracic compression.

In order to experimentally quantify the "foot-squeezing" pressure produced by birds of prey while holding their quarry, we used a measuring device which mimicked a natural prey, i.e., a wild mouse. As

far as we know, there is only one instance of this sort of measurement, in a documentary-film from the 1960s (D. Meier, *The hunters of the sky*, Italian edition). This film, produced in the USA, shows one captive temporarily blinded Harpy-eagle (*Harpia harpyja*) standing on the falconer's arm. The bird is then induced to squeeze a plastic bottle filled with water, covered with fur, and connected to a mechanical dynamometer.

METHODS

We used wild Common Buzzard ($n = 6$; 3 adults, 1 subadult, 2 immatures) and Eurasian Kestrel ($n = 11$; 4 males, 5 females, 2 juveniles) which were temporarily in captivity for rehabilitation but in perfect physical and flight condition. The sex of buzzards and of juvenile kestrels was not determined because of the difficulty of ascertaining it visually.

Using penned birds is unlikely to influence our observations of their predatory behavior. By comparison with observations of predatory attempts under natural conditions, previous studies (Csermely et al. 1989, 1991, Csermely 1994) showed that the rather close distance to the prey in captivity does not seem to affect the velocity of the bird during the glide, its impact against the prey, or the overall sequence of predatory behavior. In addition, responses to live and dead prey are similar (kestrels; Csermely 1994).

Several days before testing, each bird was treated pharmacologically for ecto- and endoparasites. The bird was then removed from its aviary, measured (mass, tarsus diameter and length, length of bill, of the first, second, and third toe and of respective talons), and assigned to an experimental pen. It remained there fasting for 48 hr before testing to enhance and, as far as possible, equalize the predatory motivation of all birds.

The test pen was $10 \times 3.5 \times 2.5$ m and was located in a small woodland. The pen was equipped with a wooden perch (1.7 m high) near the back short side. The roof of the pen had a cover over the rear third above the perch. The experimental prey was located on a plastic table ($60 \times 60 \times 60$ cm) about 1.5 m from the front side of the pen and equally distant from the long sides. The experimenter remained outside the pen in a wooden blind with a one-way window.

We constructed a dynamometer for measuring foot pressure using a rubber pipe (2.7 cm diameter, 0.3 cm thickness, 30 cm length), sealed at one end with a metal plug and filled with glycerin oil (Fig. 1). The other end of the pipe was attached to a pressure transducer

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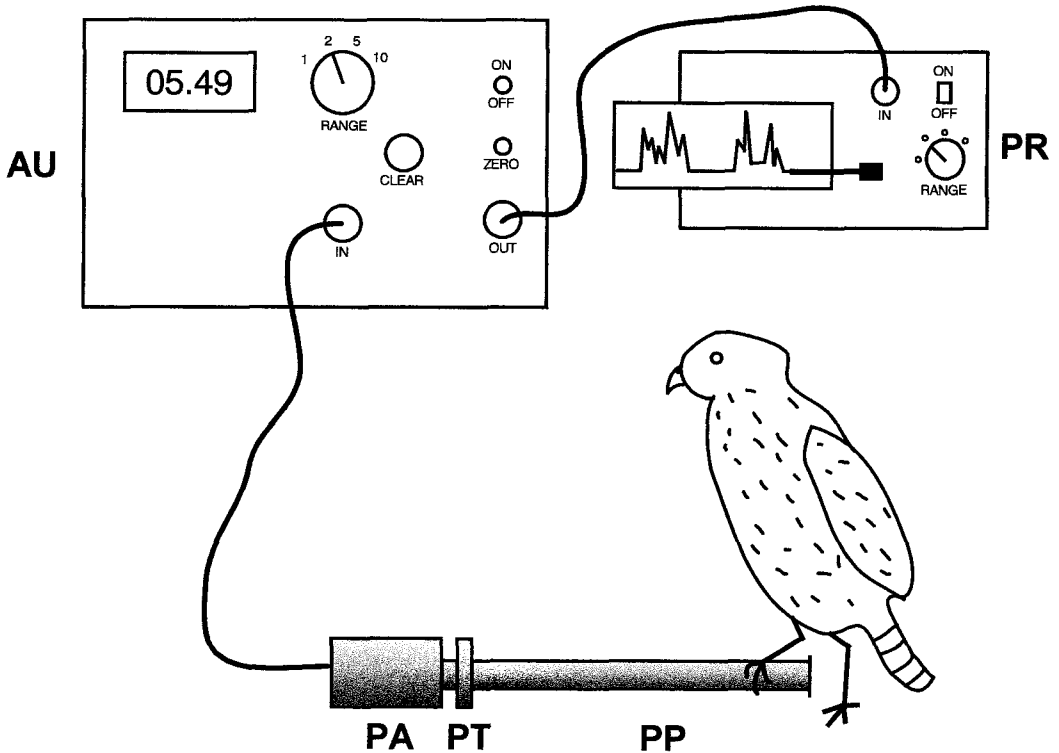


FIGURE 1. A diagrammatic view of the device used for quantifying squeezing pressure (not drawn to scale). The mouse skin surrounding the rubber pipe is not shown. AU = the amplifier unit, PR = the pen recorder, PA = the pre-amplifier, PT = the pressure transducer, PP = the rubber pipe filled with glycerin oil.

(Model P155-150G-E2A, Kavlico, Moorpark, California) that transformed foot pressure exerted on the pipe into a pre-amplified electric analogue signal. The signal was then forwarded to an amplifier unit which further amplified the signal and converted it to a numeric pressure value (kg cm^{-2}). The pressure was shown instantaneously on an LCD display and tracked by a pen recorder, producing a record of changes in pressure over time. The LCD display also stored the maximum value recorded for each test. The dynamometer was calibrated using dynamometric pliers, usually used in Physics. The upper measuring limit was 2 or 20 kg, depending on the multiplier value chosen on the amplifier unit. The values displayed by the amplifier unit at 1 sec intervals were read starting when the bird grasped the pipe until it left. The average pressure performed by the birds was considered as the mean value for that test.

The ends of the pipe were firmly attached to the platform to avoid distorted values if the bird pulled on the tube. The proximal end of the pressure transducer was covered with jute, and the closed end was covered with a laboratory adult mouse skin (C3H strain, agouti pelage), that had been tanned with NaCl.

The tests were carried out between 10:00 and 14:00. Each test lasted no more than 60 min. Each bird was tested 7 times on 7 consecutive days, with a fixed se-

quence of tests. On the first 4 days, the raptor was offered one dead adult laboratory mouse (C3H strain, agouti pelage), placed on a plastic table, to train it to an immobile prey. On the fifth day, the bird was offered the same type of prey and its predatory behavior was recorded. This was considered as the first experimental test.

On the sixth day, the test was carried out using the pressure measuring device, whereas on the seventh test the bird was offered one adult live mouse of the same strain as previously. Preliminary tests and previous observations (Csermely 1993) showed that both buzzards and kestrels behaved similarly when capturing dead or live mice. The mice used were surplus from the breeding colony of our department. After its death and just before ingestion, the mouse was taken from the raptor's feet and visually inspected to ascertain whether the pressure values measured were compatible with the hypothesis of killing by suffocation. Visual inspection of prey was conducted within 30–60 min of death.

We kept the experiment sample as low as possible ($n = 6 + 11$), compatible with the minimum requirements of the statistical analysis and birds available, in order to sacrifice as few prey as necessary. Latency and duration of behaviors were compared using the Kruskal-Wallis one-way ANOVA. A Spearman rank test was used to correlate the squeezing pressure with

the morphological characters of the bird. Unless otherwise stated, two-tailed tests were used throughout, and means are presented \pm SE.

RESULTS

BUZZARDS

The buzzards displayed similar behavior patterns during the tests. Preening, a displacement behavior indicative of conflict (Csermely et al. 1991), was never observed. All buzzards hunted prey in each test. We did not detect differences in latency of predation for different test types ($H = 1.09$, $n = 18$, $P > 0.1$). Although the prey was invariably gripped with one foot only, there was no preferred foot. The approach to the prey was indirect in both the dead-mouse tests and the dynamometer tests, that is, the bird first landed on the table and then gripped the mouse. Four birds landed directly onto the live prey. The buzzards grasped the mouse skin surrounding the rubber pipe almost invariably at the trunk, whereas one bird only gripped the mouse skin at the neck region.

The buzzards had no difficulty in grasping the pipe surrounded by the mouse skin. Their toes encircled the pipe and their talons were parallel to the pipe surface and not against it. The squeezing strength displayed by buzzards was variable over time and differed greatly between individuals. In contrast to expectation, squeezing was intermittent. The grasping technique typically consisted of repeated squeezing bouts, very limited in duration (a few seconds), and separated by prolonged intervals without squeezing (Fig. 2). The total duration of squeezing episodes varied greatly between birds. Buzzard A can be considered as an outlier and was the only one displaying one single long squeezing bout. The total mean duration of the squeezing action was 26.1 ± 5.3 sec, and the mean frequency of bouts was 2.7 ± 0.6 .

The highest peak of pressure scored was several times higher than the mean value. It was reached after a mean latency of 20.8 ± 5.8 sec, but was not correlated with the mean pressure ($P > 0.08$). The average of the maximum peak values reached by all buzzards was 5.87 ± 0.94 kg cm⁻². The mean and maximum pressure values were independent of the bird's mass (Table 1).

Three buzzards bit the fake mouse. The bites appeared to be true bites to the head, performed exactly as during tests with live or dead mice. The squeezing pressure of the bite was comparable with that of the foot in both duration (a very few seconds) and intensity. The maximum squeezing pressure did not correlate ($P > 0.05$) with any morphological variable nor with age.

The buzzards grasped live mice similarly to dead mice. The latency of predation, the grasping technique (with one foot only), and the number of bites did not differ between prey type. Visual inspection of prey revealed that the killing technique was consistent with that recorded for kestrels (Csermely et al. 1998). Two of six mice showed biting wounds on the head (ear region and, in one mouse only, cervical vertebrae breaking), whereas one had severe talon wounds in the abdominal region. Five mice showed unclotted blood after excision of large vessels. Similarly, five mice had

coronary artery dilation and pulmonary petechiae and suffusions (Dorian 1988, 1989).

KESTRELS

Similar to buzzards, kestrels did not vary their behavior patterns during the tests. In some trials we observed behavior that may have indicated conflict. One bird performed preening once, during a dead-mouse test (duration 146 sec.), and a few movements on the perch during both the dead- and fake-mouse tests. Another kestrel performed movements on the perch in every test and a third bird only during the dynamometer test.

All kestrels caught the prey in each test. Their behavior was similar to that of buzzards. The latency of predation in live-mouse tests was shorter (330.8 ± 105.0 sec) than in dead-mouse and dynamometer tests ($1,053.0 \pm 384.1$ sec and $1,068.7 \pm 364.0$ sec, respectively), but not significantly so ($P > 0.1$).

In 7 trials, kestrels grasped the prey using both feet (4 dead-mouse tests, 2 live-mouse tests, and 1 dynamometer-test). The approach to the prey was almost equally distributed between direct and indirect in each test. Only the fake-mouse test had nine indirect approaches vs. two direct ones. The kestrels grasped the mouse skin with the same technique used with "true" mice, gripping the trunk (7 tests) or the head (3 tests). One kestrel gripped the fake mouse at the hind quarter. Like buzzards, they encircled the rubber pipe with toes and talons, but did not use the talons to grip the fake mouse.

In contrast to buzzards, the squeezing pressure displayed by kestrels was rather continuous (Fig. 2), although at a much lower level. It was characterized by continuous alternations of hard and soft squeezes without returning to zero value. Despite some variability with time, a relatively continuous foot pressure was maintained against the pipe. This technique was very similar in all kestrels. One bird bit repeatedly at the fake mouse, whereas this occurred occasionally in the remaining 10 kestrels. When the mouse skin was bitten, the squeezing pressure was comparable to the pressure values given by the foot, as recorded in buzzards. On the other hand, the duration of biting was much more limited (1 to 2 sec) than foot pressure.

The mean total squeezing duration was very similar to that of buzzards (28.4 ± 4.6 sec). Kestrels scored more squeezing peaks ($n = 6.6 \pm 1.0$), although they were more difficult to ascertain because kestrels did not stop squeezing as did buzzards. The maximum pressure recorded for each bird was generally below 1 kg cm⁻², with the exception of two kestrels that squeezed up to 1.25 kg cm⁻² (Table 1). Maximum pressure values were rather similar between birds (mean 0.78 ± 0.08 kg cm⁻²). The maximum pressure was reached after a latency of 17.1 ± 4.5 sec. This value was independent of body weight ($P > 0.1$) and was several times the value of body mass (Table 1).

The kestrels' pressure was not correlated with body mass or with the maximum pressure reached by the bird itself ($P > 0.1$). Finally, neither the maximum pressure value nor the mean pressure value was correlated ($P > 0.05$) with any morphological character considered, apart from the length of the third toe talon

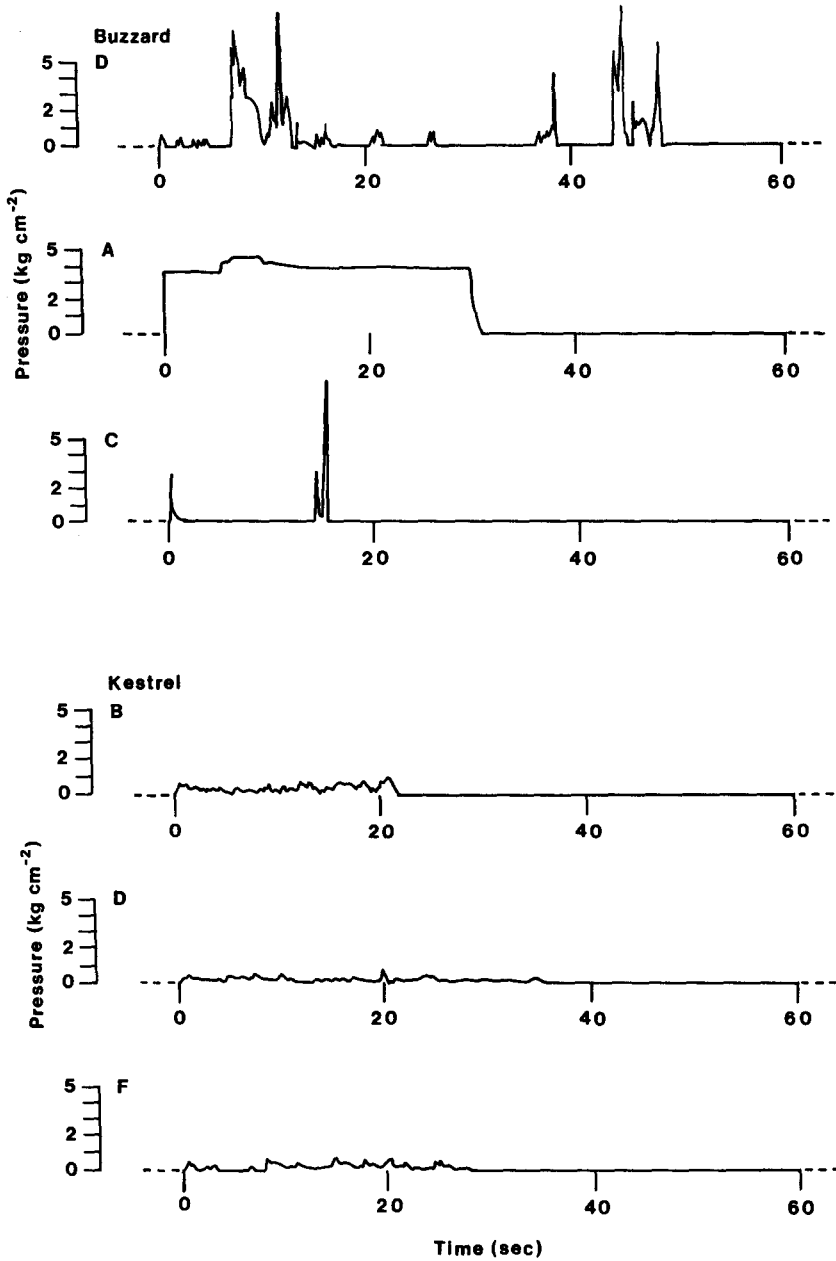


FIGURE 2. Some squeezing pressure graphs recorded in buzzards and in kestrels. The graph starts at the first contact of the bird with the pipe. The duration is fixed at 60 sec.

with the maximum pressure ($r_s = 0.75$, $n = 11$, $P < 0.02$).

As in buzzards, prey type did not affect the predatory behavior sequence. Visual inspection of the live mice showed the same signs described elsewhere (Csermely et al. 1998). The mice were always bitten on the head, almost invariably at the skull base and

more rarely at the ear region. Mice showed no wounds from talons, whereas only one had a few superficial skin abrasions on the trunk, likely caused by the foot squeezing. The internal inspection revealed no wounds to the entrails; however, one mouse had two ribs broken. Four mice showed petechiae on lung or cardiac surface and unclotted blood after the large vessels were

TABLE 1. The squeezing pressure values exerted by buzzards and kestrels during the test. The bird's mass was recorded at the beginning of the experiment. ME P/M = ratio of the mean pressure and bird's mass; MAX P/M = ratio of the maximum pressure and bird's mass.

	Age/sex	Mass (g)	Mean pressure (kg cm ⁻²)	ME P/M	Max. pressure (kg cm ⁻²)	MAX P/M
Buzzard						
A	Adult	670	3.89	5.806	4.50	6.716
B	Juvenile	660	1.32	2.000	2.75	4.167
C	Adult	700	0.66	0.943	8.25	11.786
D	Sub-adult	640	0.94	1.469	8.75	1.469
E	Juvenile	700	1.03	1.471	5.00	7.143
F	Adult	740	0.67	0.905	6.00	8.108
Mean ± SE		685.0 ± 14.5	1.42 ± 0.50	2.10 ± 0.76	5.87 ± 0.94	6.57 ± 1.43
Kestrel						
A	Adult F	180	0.18	1.000	1.12	6.222
B	Adult F	200	0.22	1.100	0.60	3.000
C	Juvenile	200	0.45	2.250	0.75	3.750
D	Adult M	160	0.16	1.000	0.87	5.438
E	Juvenile	140	0.02	0.143	0.25	1.786
F	Adult F	155	0.23	1.484	0.75	4.839
G	Adult M	177	0.40	2.260	0.75	4.237
H	Adult F	264	0.08	0.303	0.70	2.652
I	Adult M	166	0.68	4.096	1.25	7.530
J	Adult F	203	0.20	0.985	0.85	4.187
K	Adult M	168	0.12	0.714	0.65	3.869
Mean ± SE		183.0 ± 10.1	0.25 ± 0.06	1.39 ± 0.34	0.78 ± 0.08	4.32 ± 0.50

excised. In addition, six mice showed dilation of coronary arteries.

DISCUSSION

The lack of statistical difference between the behavior patterns displayed before the attack and between the latency of predation shows that buzzards and kestrels reacted to the mouse skin similarly to the live or dead mouse (Csermely 1993). This allows us to extrapolate our data to natural predation attempts.

The data from visual inspections are consistent with suffocation (Csermely et al. 1998) after foot squeezing as the primary cause of death by both raptor species. The almost constant presence of unclotted blood, together with pulmonary and cardiac petechiae and suffusions with coronary artery dilation, is interpreted by forensic medicine as a death by suffocation in humans (Chiodi et al. 1976, 1977, Canuto and Tovo 1992, Macchiarelli and Meola 1995). We think it reasonable to extend such a finding to rodents as well. If we assume that the grasp of our raptors to the fake mouse is the same as to real mice, then our data are consistent with a squeezing pressure so strong as to cause suffocation.

In order to confirm this finding, we need to ascertain whether the pressure values are strong enough to prevent chest expansion. Buzzards exerted very high pressure values (up to more than 8 kg cm⁻²), although of short duration and well separated by lack of squeeze. Because the bird's toes completely encircle the rodent's chest, the values recorded must be considered as applied to the whole chest surface. The Harpy-eagle showed in the documentary film cited earlier performed a squeezing pressure of 11.3 kg cm⁻², i.e., ap-

proximately 14% more than the maximum pressure performed by our buzzards. Considering that the Harpy-eagle is several times larger than the buzzard, we can easily understand how strong is the pressure exerted by the buzzard against the mouse. Thus, the buzzard's strength is capable of thoracic compression.

Because they were at least a third the buzzard's mass and with thinner legs and toes, kestrels exerted less pressure than buzzards, remaining generally well below 1 kg cm⁻². We do not know whether such a pressure is enough to block chest expansion. This hypothesis could be verified experimentally by applying a known pressure to a live mouse's chest. Although thoracic compression is considered a humane technique of euthanasia for small mammals (American Society of Mammalogists 1987), we chose not to kill additional rodents simply to measure this pressure. The values we measured are probably not sufficient to prevent breathing directly. Kestrels probably compensated for reduced strength by squeezing for longer periods of time. Buzzards need not squeeze for a prolonged period because their intermittent squeezing bouts are sufficiently strong to induce fatal cardiopulmonary compression.

In contrast to the squeezing technique used by the two raptor species, grasping duration after capture is surprisingly similar. Kestrels likely needed that time to induce death to their quarry by continuous squeezing, whereas buzzards presumably held it during that time to confirm that their occasional squeezes had killed the prey. The absence of any correlation with morphological variables shows that foot squeezing strength is independent of body size within each species.

In previous findings (Csermely 1993, 1994, Cser-

mely et al. 1998), the bites performed to the head appeared to limit prey movements and escape attempts by damaging the central nervous system, but were not a killing method. If so, bites would be expected to occur only when live prey are caught. In the present study, however, both buzzards and kestrels performed some bites toward immobile prey (see also Cade 1982). Csermely (1993) hypothesized that biting, although originally released only by prey movements, later became a fixed part of capture behavior. Thus biting would occur with a lower frequency in any capture, but prey movements should release additional bites targeted to the occipital region. Consistent with this hypothesis, live mice elicited higher biting frequencies in our study. Moreover, kestrels bit more frequently than did buzzards, which is consistent with kestrels having more difficulty subduing prey by foot squeezing pressure alone. Interestingly, in studies of different prey sizes, larger prey elicited more biting activity in the same raptor species (Csermely 1994, Csermely et al. 1998).

Our observation of grasping action performed to the fake mouse by both buzzards and kestrels together with the visual inspections confirmed previous observations that talons were not used to kill the rodents (Csermely et al. 1998). In fact, neither species used talons to grip the pipe or as a killing weapon. In contrast to the stabbing behavior reported by Cade (1982) as typical of Accipitridae, we did not record any use of talons in buzzards. Talons also could have evolved as a means to elongate the toes to get a bigger surface to contact the quarry (Csermely et al. 1998).

Finally, although kestrels are sexually size dimorphic, there was no difference between sexes in the technique used to hold the prey or in the amount of foot pressure. Our data confirm Balgooyen's (1976) conclusions on the American Kestrel (*Falco sparverius*) that they hunt primarily on prey which correlate with the bird's predation weapons and not with body size. This fact can be usefully taken into account when evaluating the differences in type of prey captured by either sex (Eurasian Kestrel: Bryan 1984, Village 1990; American Kestrel: Bildstein and Collopy 1987, Meyer and Balgooyen 1987). The bias in prey taken by either sex would then be determined not by different ability to subdue the quarry but by different winter habitat use (Meyer and Balgooyen 1987), different capacities of carrying prey (Southern 1974), or energetics (Korpimäki 1985).

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