Ecologists are beginning to appreciate the complex energetic links between aquatic and terrestrial systems (Baxter et al. 2005). It has been estimated that in some riparian systems, 25–100% of the energy and carbon budgets of terrestrial birds, bats, lizards, and spiders can be derived from aquatic insects. Most studies of energy and nutrient fluxes from aquatic to terrestrial ecosystems have focused on the smaller insectivorous passerine birds (reviewed by Baxter et al. 2005). Our focus is on the importance of insects, specifically the California Stonefly (Pteronarcyis californica), in the diet of the Peregrine Falcon (Falco peregrinus).

The California Stonefly, following a year of embryonic development and another four years in aquatic larval stages (Townsend and Pritchard, 1998), emerges as an adult and swarms in western North America from mid-April to early August. The largest swarms on the Blackfoot and Gallatin rivers occur during June. Because emergences of stoneflies and other aquatic insects tend to be extremely synchronous, these can provide predictable and significant, albeit typically brief, pulses of concentrated food.

We first observed adult peregrines capturing California Stoneflies (commonly known as salmonflies) on 9 June 2004 near the falcons’ eyrie along the Blackfoot River across from Johnsrud Park in Missoula County, Montana. Using spotting scopes from a distance of 60 to 100 m, we watched two feeding bouts in the early afternoon (Table 1). In the first instance, the adult female circled about 15–80 m over the river near the nesting cliff and made shallow dips along her flight path. With each dip, she captured a stonefly in her talons and, without pause, transferred it to her beak and swallowed it whole. Figures 1, 2, and 3 show the adult female Peregrine Falcon approaching, catching, and transferring a stonefly to her beak. During the 3-minute flight, the female captured 23 stoneflies with no apparent misses before landing out of sight on the cliff (Table 1). The average time between captures was 8 seconds. The stoneflies were emerging in large numbers, and the high rate of capture we observed may have been directly related to the density of the insects.

In the second foraging bout, we observed the adult male, in the same manner, capture 14 stoneflies over the course of the 2.5-minute flight. He missed one stonefly during this flight, and averaged a capture every 11 seconds. Afterward, the male flew to the eyrie and remained there for slightly more than 1 minute, then flew out of sight down the river. During this visit, we were unable to see either of the two 3-week-old young because they were out of view at the back of the nesting ledge.

During 2007, we observed 15 foraging flights by Peregrine Falcons at two eyries along the Blackfoot River near Bonner and Johnsrud Park. Observation distances ranged from 50 to 200 m. The foraging flights varied in duration from 1.5 to 29.5 minutes. We counted the number of stoneflies captured per minute during six of these flights (Table 1). The intervals between captures ranged from 3 to 128 seconds. The feeding bouts occurred during emergences of the California Stonefly and two other species of stonefly, the Elongate Springfly (Isogenoides elongatus) and Golden Stone (Hesperoperla pacifica). The larger California Stonefly ranges in length from 38 to 76 mm. The Elongate Springfly (length 15–20 mm) and the Golden Stone (length 19–30 mm) are much smaller.
Figure 1. Adult female Peregrine Falcon approaching a stonefly (located in upper right corner of photo).

Photo by Kate Davis

Figure 2. Adult female Peregrine Falcon catching a stonefly.

Photo by Kate Davis
On 8 June 2007 (13:20), we observed the adult male Peregrine Falcon near Bonner capturing and eating stoneflies. He appeared to be selecting the largest stoneflies ascending from the river. At the peak of his foraging flights, the male consumed three to four stoneflies per minute. Later (14:30–17:08), the adult female made 11 separate foraging flights for stoneflies, returning to the nesting cliff after each flight. We were able to establish a capture rate of four flies in 1.5 minutes during only one of these foraging bouts.

On 9 June 2007 (12:12), the male Peregrine near Bonner was again foraging on stoneflies. Other raptors were also observed feeding on the stoneflies as their

Table 1  Rates of Capture of Stoneflies and Estimated Caloric Intake during Eight Foraging Flights by Adult Peregrine Falcons

<table>
<thead>
<tr>
<th>Date</th>
<th>Sex</th>
<th>Location</th>
<th>Time</th>
<th>Duration (min)</th>
<th>Stoneflies captured</th>
<th>Rate (number/min)</th>
<th>Estimated energy intake (cal/min)</th>
</tr>
</thead>
<tbody>
<tr>
<td>9 Jun 2004</td>
<td>F</td>
<td>Johnsrud Park</td>
<td>14:15</td>
<td>3</td>
<td>23</td>
<td>8</td>
<td>960</td>
</tr>
<tr>
<td>9 Jun 2004</td>
<td>M</td>
<td>Johnsrud Park</td>
<td>14:19</td>
<td>2.5</td>
<td>14</td>
<td>6</td>
<td>720</td>
</tr>
<tr>
<td>8 Jun 2007</td>
<td>M</td>
<td>Bonner</td>
<td>13:20</td>
<td>10.5</td>
<td>22</td>
<td>2</td>
<td>240</td>
</tr>
<tr>
<td>8 Jun 2007</td>
<td>M</td>
<td>Bonner</td>
<td>14:30</td>
<td>1.5</td>
<td>4</td>
<td>3</td>
<td>360</td>
</tr>
<tr>
<td>9 Jun 2008</td>
<td>M</td>
<td>Bonner</td>
<td>12:12</td>
<td>5</td>
<td>14</td>
<td>3</td>
<td>360</td>
</tr>
<tr>
<td>9 Jun 2007</td>
<td>M</td>
<td>Bonner</td>
<td>12:38</td>
<td>29.5</td>
<td>51</td>
<td>2</td>
<td>240</td>
</tr>
<tr>
<td>11 Jun 2007</td>
<td>M</td>
<td>Johnsrud Park</td>
<td>13:41</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>120</td>
</tr>
<tr>
<td>19 Jun 2007</td>
<td>F</td>
<td>Storm Castle</td>
<td>16:30</td>
<td>1.7</td>
<td>7</td>
<td>4</td>
<td>480</td>
</tr>
</tbody>
</table>

*On the basis of a rough estimate of 800 cal/g wet weight of stoneflies (average wet mass 0.15 g).*

Figure 3. Adult female Peregrine Falcon transferring stonefly to her beak.

*Photo by Kate Davis*
front of emergence moved upstream. An American Kestrel (*Falco sparverius*) flew from a perch several times to catch insects, returning to the perch to feed. Later, the kestrel made longer foraging flights and began transferring the stoneflies to its bill in mid-air in the same manner as the Peregrine Falcons. Two Red-tailed Hawks (*Buteo jamaicensis*) foraged similarly on the stoneflies. Finally, two non-resident Peregrine Falcons joined in, and the mixed group of raptors fed simultaneously on the emerging insects, often at heights of over 100 m. Eventually, the raptors disappeared around a bend in the river, following the insects’ front of emergence.

We again observed both adult Peregrine Falcons from the Johnsrud eyrie hunt the stoneflies on 11 June 2007. On 19 June 2007, we observed the adult female at the Storm Castle eyrie perform similar foraging flights over the Gallatin River near Bozeman, Montana. Here, the adult female was joined by four Common Ravens (*Corvus corax*). The ravens also caught the stoneflies in mid-air, but, unlike the peregrines, they captured the stoneflies directly with their beaks.

To estimate the energetic rewards of this foraging strategy, we captured some emerging stoneflies and measured their fresh wet mass on a Mettler Toledo balance. The average wet mass of stoneflies was 0.15 g (*n* = 16). As a rough estimate of the caloric value of the stoneflies, we used 800 cal/g for wet weight (Cummins and Wuycheck 1971). The peak observed capture rate of eight stoneflies per minute would result in an energy gain of about 960 cal/min, but lower capture rates of two to three flies per minute would still provide substantial energy rewards of 240–360 cal/min.

The Peregrine Falcon feeds primarily on birds but does, on occasion, take insects (White et al. 2002). Sherrod (1983) observed recently fledged peregrines capturing mostly butterflies and found remains of insects of the orders Coleoptera, Lepidoptera, and Odonata in pellets. In the only observation described, an adult bird captured and ate a large beetle. Pruett-Jones et al. (1980) also reported cicadas (Hemiptera) and grasshoppers (Orthoptera) as prey in peregrine eyries in Australia. Craig and Enderson (2004) saw perched adult Peregrine Falcons feeding on Mormon Crickets (*Anabrus simplex*) as they swarmed past their nesting perch. White et al. (2002) listed insects as uncommon food items, with most records coming from the orders Orthoptera (grasshoppers and crickets) and Odonata (dragonflies and damselflies). White and Brimm (1990) described once seeing a male Peregrine Falcon in Fiji catching locusts. White (pers. comm.) also believes Peregrine Falcons take the African flying termites (alates), because they are so common and are reported to be major food items of other African falcons, the African Hobby (*Falco cuvieri*), the Red-footed Falcon (*Falco vespertinus*), and the Amur Falcon (*Falco amurensis*), as reported by Brown et al. (1982). In Oregon, Henny and Pagel (2003) recorded four species of insects as Peregrine Falcon prey and observed adults and subadult Peregrine Falcons catching swarming mayflies. Ellis et al. (2007) reported 91 distinct incidents of predation on insects by adult Peregrine Falcons during 11 feeding bouts in Arizona. Cicadas (family Cicadidae) were identified as the prey in 41 (69%) of these.

We found no accounts in the literature of peregrines feeding on insects of the order Plecoptera (stoneflies). Our observations, however, suggest that Peregrine Falcons breeding along rivers forage on the pulsed emergences of large species of stoneflies routinely, and that this opportunistic foraging strategy likely results in substantial energy rewards.

We owe special thanks to Erick Greene who observed and tallied the stonefly capture rates during many of the 2007 Peregrine Falcon foraging flights. In addition, Erick weighed the stoneflies, calculated the caloric intake values, and wrote the introduction and methodology related to caloric intake. Sally Phillips helped with the counting of stoneflies captured at Johnsrud Park. Kathy Fewlass and Byron Crow assisted with the counts at Johnsrud Park in 2004. Montana Fish, Wildlife and Parks, the U.S. Fish and Wildlife Service, the Bureau of Land Management, the Bureau of Indian Affairs, the Bureau of Reclamation, the U.S. Forest Service, Raptors of the Rockies, and the
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LITERATURE CITED


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