

1 ■Title

2 Fish-Hunting by Wild Japanese Macaques in Riverine Environments: Behavioral  
3 and Demographic Patterns with Implications for Sex-Invariant Foraging in Early  
4 Hominins

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32

## ■Abstract

Fish-hunting, rare among nonhuman primates, has been hypothesized to markedly influence hominin evolution. We report 71 cases of fish-hunting by wild Japanese macaques (*Macaca fuscata*) inhabiting a subalpine riverine environment. Behavioral sequences were categorized into the exploration, attempt, and processing phases. All events were solitary and tool-free. No behavioral evidence indicated the facilitation of successful fish catching by conspecific presence. Most preyed fish were salmonids, and nearly all were fully consumed. Significant sex differences in fish-hunting frequency were not observed, and certain juveniles also engaged in fish catching. The absence of visible bone remains in fecal samples with confirmed fish DNA suggests that tool-free fish consumption leaves limited archaeological traces. These findings provide novel comparative data on primate aquatic foraging and suggest the feasibility of solitary, non-tool-assisted fish-hunting under certain ecological conditions, offering new perspectives on early hominin subsistence strategies.

## ■ Introduction

The earliest evidence of aquatic fauna consumption by early hominins dates to approximately 3.0–2.6 million years ago<sup>1</sup>. The proposed role of aquatic fauna as animal-based food sources in hominin diets reflects post-bipedalism dietary shifts<sup>2</sup>. The oldest archaeological evidence of fish consumption dates to approximately 1.95 million years ago during the early Pleistocene<sup>3</sup>. Among aquatic fauna, fish are particularly rich in long-chain polyunsaturated fatty acids, including eicosapentaenoic and docosahexaenoic acids, compared to terrestrial fauna. The proposed contribution of fish consumption to early brain volume expansion in the genus *Homo* has been linked to its nutritional profile<sup>4</sup> (but see<sup>5</sup>). Despite the hypothesized significance of fish consumption in hominin evolution, evidence remains scarce regarding the origins, diffusion, capture strategies, and demographic patterns of fish-hunting individuals.

To better understand the evolutionary trajectory of human behavior, biological anthropology has long utilized behavioral comparisons with extant nonhuman primates<sup>6,7</sup>. However, many primate species range from arboreal to predominantly terrestrial lifestyles, and only a small proportion—approximately 10% (~30 species)—regularly interact with aquatic environments<sup>8</sup>. Reports of

fish consumption among extant nonhuman primates remain scarce. Based on a list of studies addressing the consumption of aquatic fauna by nonhuman primates<sup>8–11</sup>, we compiled a comprehensive literature survey on fish-catching and consumption in non-human primates (Table 1; <sup>12–28</sup>). Including suggestive evidence such as opportunistic observations by field assistants in wild and captive settings, fish-catching and/or consumption have been reported in 13 primate species to date. Among these, only seven species have been documented to catch and consume live fish under natural conditions.

These findings from nonhuman primates offer important insights: fish may function as a fallback food when other resources are scarce<sup>17, 21</sup>; fish-eating behavior may be socially transmitted within groups<sup>15</sup>; and, in some cases, tool use accompanies fish-hunting<sup>10</sup>. However, consistent patterns across ecological or behavioral factors remain elusive. While this may reflect phylogenetic differences across species or ecological and genetic variations within species, several methodological and contextual limitations challenge broad interpretations. For instance, some studies report only a handful of fish-hunting events over extensive observation periods (e.g., three cases over 20,000 observation hours in long-tailed macaques<sup>17</sup>). Others document substantial

anthropogenic influence, such as individuals exploiting discarded fish or using fishing tools left behind by humans<sup>9</sup>. Furthermore, in orangutans—a species with relatively frequent fish-hunting reports—provisioning is common, and individuals often refrain from consuming their captured fish<sup>10</sup>. These issues complicate biological anthropological efforts to understand the adaptive significance and evolutionary origins of fish consumption in the human lineage.

Against this backdrop, the present study focuses on a wild population of Japanese macaques (*Macaca fuscata*) in Kamikochi, central Japan, where individuals have been observed catching and consuming live fish from both a flowing river and spring-fed pools with a relatively high frequency since 2021. This unprovisioned population offers a rare opportunity to investigate fish-hunting behavior under natural foraging conditions. In 2021, a molecular dietary analysis revealed the presence of salmonid DNA in 7 out of 38 winter fecal samples collected from this group<sup>13</sup>. Subsequent direct behavioral observations and camera-trap footage confirmed winter fish-hunting by these macaques, with such events occurring at a relatively high frequency<sup>12</sup>.

This study investigates the behavioral traits (e.g., presence or absence of tool use and cooperation in hunting) and demographic factors (e.g., sex differences

and developmental variation) associated with fish-hunting behavior in a wild population of Japanese macaques in Kamikochi. Through analysis of behavioral patterns and demographic factors among fish-hunting individuals, this study clarifies the origins and diffusion of fish consumption in primates.

Despite accumulating anecdotal reports, systematic data on sex-specific fish-hunting patterns in wild primates remain sparse. In particular, sex differences in hunting behavior are central to anthropology for their potential to inform the evolutionary origins of the sexual division of labor in human societies<sup>29</sup>. Among our closest living relatives, chimpanzees, red colobus monkey hunting and the exploitation of aquatic faunal resources—exemplified by crab fishing—occur more frequently in males and females, respectively<sup>30,9</sup>. These findings corroborate patterns observed in extant human foraging societies—male-biased hunting frequency and female targeting of more predictable<sup>31</sup>. These patterns have led to the hypothesis that sex differences in aquatic resource exploitation existed in the hominin lineage<sup>9</sup> and that hunting disparities may have preceded the evolution of the sexual division of labor in modern humans<sup>30</sup>. Despite these insights, consistent patterns of sex differences in fish-hunting behavior among nonhuman primates remain unidentified (Table 1). Therefore, detailed

quantitative analyses of sex-specific fish-hunting patterns are needed to clarify the origins of hunting-related sex differences, including those related to aquatic resource exploitation, and the evolutionary sexual division of labor. The Japanese macaques of Kamikochi, with observable and measurable variations in fish-hunting behavior in the wild, offer a valuable model to address this gap.

## ■Methods

### Study site

This study was conducted in Kamikochi, located in the city of Matsumoto, Nagano Prefecture, Japan. Kamikochi lies within the Chubu Sangaku National Park and is situated in a subalpine zone at ~1,500 m above sea level. The Azusa River, which runs through Kamikochi, is characterized by an extremely gentle gradient of ~8‰, rising only 80 m over a 10 km stretch from 1,490 m to 1,570 m. This topography partly results from historical volcanic activity in the region<sup>32</sup>. In addition, numerous springs throughout the area ensure the year-round presence of small streams and pools, even during the winter season. Kamikochi is also a popular tourist destination, attracting over 1 million visitors annually. As a result, local Japanese macaques (*Macaca fuscata*) are human-habituated



without intentional provisioning, enabling direct behavioral observation and continuous tracking. The area thus provides a unique opportunity to conduct detailed field observations of wild primates, even under severe winter conditions.

### **Study period and observation methods**

Direct behavioral observations were conducted for two winter periods: 19–30 January 2022 and 11 January–22 February 2023. The total number of observation days was 50. Each day, observers (the authors) conducted fieldwork from approximately 09:00 to 16:00, either in a single group or divided into two teams. The observational subjects comprised three groups of wild Japanese macaques inhabiting the Kamikochi region. These groups were designated as KT, KK, and KM, in order from west to east based on their ranging areas. The home ranges of the KT and KK groups—and those of KK and KM—were either overlapping or adjacent.

Researchers searched for signs of macaque presence (e.g., footprints and feeding traces) while driving a survey vehicle along the main road. Upon detecting such signs, the macaques were located by tracking on foot. Once

located, each group was followed, and when individuals appeared near aquatic environments—such as rivers or pools—the protocol shifted to individual-following for detailed behavioral monitoring<sup>33</sup>.

To maximize fish-hunting observation opportunities, researchers prioritized tracking groups located in riverine areas. When a followed group moved away from aquatic locations, the observers occasionally discontinued the follow and searched for other groups instead.

Behavioral events near aquatic habitats were recorded using high-definition video equipment, including a 4K 2/3-type 3-chip CMOS shoulder-mount camcorder (PXW-Z750, SONY), a 4K expert handy camera (FDR-AX100, SONY), and a Phantom Flex4K digital cinema camera (Flex4K, PHANTOM).

## **Definition of fish catching and dataset**

From the collected video footage, we extracted instances of visible interactions between Japanese macaques and fish, including cases with clearly discernible fish bodies or silhouettes. Fish-catching was operationally defined as the successful transfer of a fish by a macaque from below the water surface to physical control, typically by hand or mouth, at or above the surface. Each fish-

174 hunting event was defined as a behavioral sequence comprising at least one  
175 fish-catching act. Multiple fish-catching acts occurring within a 10-second  
176 interval were classified as a single event—for example, repeated attempts  
177 involving escape and recapture were counted as one fish-hunting event.  
178 In total, we recorded 57 fish-hunting events during focal follows. We  
179 incorporated footage previously reported by Takenaka *et al.*<sup>12</sup>, comprising six  
180 focal-follow events and eight camera-trap recordings. The final dataset included  
181 71 fish-hunting events used for detailed behavioral analyses.

### 182 183 **Individual identification, group assignment, and fish species identification**

184 During group follows, individual identification was conducted for macaques  
185 bearing conspicuous physical features, such as scars, or equipped with VHF  
186 radio collars attached to at least one adult female per group<sup>34</sup>. Group identity  
187 was inferred based on confirmation of these individually identified macaques.  
188 For camera-trap footage, when individually recognized macaques appeared,  
189 group identity was inferred based on the identified individual's known group  
190 membership. Camera-trap videos recorded within a 1-h interval were also  
191 considered representative of the same group. Finally, fish species observed

above the water surface were identified based on body markings and the remains left uneaten by the macaques.

### **Determination of sex and age class**

Age was estimated based on physical features, such as body size, and comparison with individuals of known age. Infants were defined as individuals estimated to be within their first year of life. Adults were defined as individuals judged to be at least five years without hair on the sexual skin; all remaining individuals were classified as juveniles.

Macaques with visible testes were classified as male. Individuals whose genital regions could be clearly observed but lacked visible testes were classified as females. In addition, individuals with elongated nipples or those observed nursing young were identified as adult females. Individuals not meeting any of these criteria were categorized as sex unknown.

### **Group composition data collection**

To assess the sex and age composition of each group during the 2023 observation period, observers conducted full group scans when many

individuals were resting or grooming together. The observers walked along the edge of the group and counted individuals from one end to the other. When individually identified macaques were not encountered during these scans, their presence was added to the total group count. Due to the need for rapid counts during stationary periods, sex was recorded only for adults; subadult and juvenile sex were not determined.

## **Analysis of sex differences in fish-hunting behavior**

To assess sex differences in fish-hunting behavior, we compared the sex ratio of fish-hunting adults with each group's overall adult sex ratio using Fisher's exact test. All statistical analyses were performed using R software<sup>35</sup>.

## **■ Results**

### **Overview of observed fish-hunting events**

Among the 71 documented fish-hunting events, 57 were conducted by adults, 8 by juveniles, 6 by subadults, and none by infants. All events were solitary and tool-free.

Each event was classified into exploration, attempt, and processing phases based on pre- and post-capture behavioral sequences. We compiled an ethogram of behavioral elements observed at least once in each phase (Figure 1).

### **Exploration phase**

In five of the 71 fish-hunting events, another individual—an infant in three events, a subadult in one, and an adult in four—was observed within 3 m of the focal animal at the moment of fish catching. An additional seven events involved another individual appearing within 10 m of the focal animal (all adults), within a visible range of the fish-catching action. However, variation in the video field of view may have led to underestimation of fish-hunting events involving nearby individuals.

In the 10 events where another individual was visibly present within the observable range, no evidence indicated a positive effect of others on fish-catching success. For example, no instances were observed of one individual capturing a fish flushed by another or of a fish being driven toward another macaque in a seemingly cooperative manner.

Transitions between aquatic foraging behaviors, such as feeding on aquatic plants or aquatic insects, and the fish-exploration phase occurred seamlessly.

Several instances of supplanting at aquatic sites were observed during the exploration phase—involving, presumably, dominant male and female individuals. Here, supplanting refers to one individual displacing another from a location or resource, typically without overt aggression but implying a dominance relationship.

Because many exploration-phase behaviors could not be conclusively attributed to fish targeting, attempts were not reliably countable; consequently, fish-hunting success rates could not be calculated.

### **Attempt phase**

During the attempt phase, the estimated body lengths of the targeted fish were approximately 5–20 cm. Based on distinctive body markings, 15 individuals were identified as salmonids. In only one case, an adult female was observed catching a *Rhynchocypris lagowskii*. No fish species other than salmonids and *Rhynchocypris* were recorded.

## Processing phase

During the processing phase, no bone- or head-removal behavior was observed regarding the captured fish. In four instances—three involving adult females and one involving an adult male—the captured fish escaped from the surface back into the water during the manipulation process. In a separate case, an adult female repeatedly bit and spat out a captured *Rhynchocypris* fish, ultimately discarding it with minimal consumption. Skin-removal behavior was observed in a single instance, and the discarded skin was not consumed. Excluding these cases, the remaining 66 events involved the full consumption of the captured fish. Notably, even in fecal samples that later tested positive for fish DNA via metabarcoding, fish bones were not visually identifiable. No direct inter-individual food transfer was observed during the processing phase. In one instance, immediately after an adult female captured a fish, another adult female approached her at close range. The fish-capturing individual quickly moved away, and the fish was not taken. This was the only observed case that suggested a potential risk of conspecific interference, although no actual scrounging or food transfer occurred.



## **Sex and age composition**

Figure 3 presents the sex–age composition of individuals involved in fish-hunting events and the overall group composition across the three study groups. No significant difference was found between adult males and females in the number of fish-hunting events or in their proportions within each group (Fisher’s exact test,  $p > 0.5$ ). Fish-hunting behavior was observed in all three groups (KT, KK, and KM). While many events involved individuals with unconfirmed identities, fish-hunting was documented in at least six adult males and seven adult females. The youngest individuals of both sexes observed catching fish were estimated to be 3 to 4 years old, although their exact age could not be determined.

## **■Discussion**

This study provides the first detailed account of the behavioral characteristics and demographic factors associated with fish-hunting in wild nonhuman primates under natural conditions (see Table 1). Our findings highlight several notable features: (i) no tool use or overt cooperation was observed; (ii) captured

fish were typically consumed in their entirety; (iii) no clear sex differences were found in fish-hunting frequency among adults; (iv) predispersal males also engaged in fish hunting. Japanese macaques exhibit a broad dietary repertoire encompassing plant and animal foods<sup>36</sup>, a relatively terrestrial lifestyle among primates<sup>37</sup>, and a capacity to inhabit cold, temperate environments<sup>38</sup>. These characteristics parallel key aspects of human ecological flexibility. In addition, as demonstrated in this study, their relatively frequent engagement in fish-hunting—rare among extant nonhuman primates—positions Japanese macaques as a valuable comparative model for understanding the evolutionary roots of aquatic resource exploitation, alongside great apes and baboons<sup>39</sup>.

### **Behavioral traits of fish-hunting**

Across all observed instances of fish-hunting, no tool use was documented. Although other individuals were occasionally present near the focal animal during fish-catching, successful captures also occurred in solitary contexts. Moreover, no behavioral evidence suggested that the presence of conspecifics positively influenced hunting success. Discussions of hominin hunting behavior have emphasized tool use<sup>40</sup> and cooperative strategies rooted in advanced

cognitive capacities linked to encephalization<sup>41</sup>. However, our findings suggest that neither tool use nor cooperation is necessary for successful fish-hunting in riverine environments.

To the extent identifiable, nearly all fish consumed by Japanese macaques were salmonids. In Kamikochi, three salmonid species have been confirmed: white-spotted charr (*Salvelinus leucomaenis*), brook trout (*Salvelinus fontinalis*), and brown trout (*Salmo trutta*)<sup>42</sup>. Although the salmonid family was identifiable from behavioral footage, species-level identification remained unfeasible<sup>43,44</sup>.

When a Japanese macaque captured a non-salmonid fish, *Rhynchocypris lagowskii* (a cyprinid species), the individual displayed aversive behaviors and ultimately discarded the fish after minimal consumption. The bile from cyprinid fish contains cyprinol sulfate, a compound toxic to mammals<sup>45</sup>, suggesting that the macaque's rejection results from a response to taste or toxicity. This case provides potential evidence for species-specific dietary selectivity in Japanese macaques' fish consumption.

### **Demographic factors of fish-hunting**

Previous studies on fish-hunting in nonhuman primates have not identified

consistent patterns regarding sex or age class (Table 1). Our current analysis of 71 fish-hunting events revealed no significant sex differences in fish-hunting frequency among adult Japanese macaques. Although the observed fish-hunting frequency in younger individuals (estimated to be 3–4 years old or older) was lower than would be expected based on group composition, these juveniles did engage in successful fish-catching. No fish catching was observed in infants (0–2 years old), although several events involved an infant being within 3 m of the focal fish-catching individual. Such close-range exposure may offer opportunities for social learning, potentially contributing to the emergence of successful fish-hunting behavior by ages 3–4.

A key direction for future research is the complete identification of all individuals in the Kamikochi macaque population. This would allow researchers to investigate whether fish-hunting frequency varies by individual or matriline, and whether individual-level differences exist in the behavioral repertoire associated with fish-hunting (see Figure 1).

### **When and how fish-hunting behavior emerged and spread**

Long-term studies of Japanese macaques in Kamikochi have been ongoing

since 1986, including home-range tracking using collar-mounted radio transmitters<sup>34</sup>. However, direct behavioral observations during winter were rarely conducted. Prior to the 2021 report of fish consumption via fecal metabarcoding<sup>13</sup>, fish-catching and consumption had remained undocumented in this population.

Although the exact emergence location and spread extent of fish-hunting behavior remain unclear, Kamikochi's unique geographical-geological characteristics—such as flat riverbeds formed by dammed lakes from volcanic activity and the presence of spring-fed streams that remain unfrozen in winter—may have created ecological conditions facilitating the innovation of fish-hunting behavior<sup>12</sup>. As in the case of the Koshima macaques, where the consumption of dead fish spread rapidly within the group (with 75% of individuals engaging in the behavior within seven years of its initial observation in 1979<sup>15</sup>), fish-hunting in Kamikochi may also have spread socially within groups after its innovation. Moreover, the fish-hunting presence across all three study groups suggests potential intergroup transmission. Given typical male Japanese macaque dispersal around age five<sup>46</sup>, fish-hunting observation by predispersal males is particularly suggestive. While primate behavioral

innovations may undergo loss and reinvention<sup>47</sup>, our findings support the potential intergroup spread of fish-hunting innovation via dispersing males<sup>48</sup>.

### **Implications for hominin evolution**

This study offers three main insights into the potential behavioral ecology of early hominins regarding fish-hunting.

First, unlike baboons often leaving behind fish bones or skin post-feeding<sup>21</sup>, Japanese macaques in Kamikochi typically consume fish entirely. Fish bones were also visually unidentifiable even in fecal samples that later tested positive for fish DNA via metabarcoding. As recent studies emphasize the importance of evaluating the archaeological visibility of tool-free foraging behaviors in extant primates<sup>49</sup>, our findings suggest that tool-free fish consumption leaves minimal or no archaeological traces<sup>50</sup>. This implies that the contribution of fish to hominin diets may be underestimated in the archaeological record and supports the hypothesis that fish consumption was more widespread than previously thought, possibly predating the earliest known evidence of fish use by hominins at 1.95 million years ago<sup>10</sup>.

Second, transitions between foraging on aquatic insects and plants and the exploration phase of fish-hunting were observed to occur fluidly without clear behavioral boundaries. This supports the hypothesis that the consumption of more readily accessible aquatic organisms, such as aquatic insects and plants, may have served as a preadaptive stage from which tool-free fish-hunting behavior subsequently emerged<sup>51</sup>. Stable carbon isotope analyses of pedogenic carbonates, isotopic reconstruction of diet from tooth enamel, and taxonomic frequencies of bovids suggest that hominin activities happened in woodland grasslands, grassland–woodland mosaics, and shrublands along riverine valleys within humid savanna biomes rich in C<sub>4</sub> grasses and herbaceous vegetation<sup>1</sup>. In such ecologically diverse and riverine environments, fish-hunting may have developed as a routinized behavior in early hominins, without requiring tool use or cooperation, following the acquisition of more easily accessible aquatic organisms such as aquatic insects and plants. The observation of predispersal individuals (juveniles) performing fish-hunting suggests potential behavioral transmission across groups via dispersing individuals, facilitating the spread and maintenance of the behavior.

Finally, our findings challenge two influential hypotheses concerning the evolution of sex foraging differences. One hypothesis suggests that sex differences in aquatic resource exploitation exist in the hominin lineage<sup>9</sup>. Another proposes that sex differences in hunting preceded the emergence of the human sexual division of labor<sup>30</sup>. In contrast to these ideas, we found no significant sex differences in fish-hunting among adult male and female Japanese macaques. Existing data on fish consumption in nonhuman primates also show no consistent patterns of sex differences. Our findings therefore suggest that female primates, including humans, are not universally risk-averse even in foraging contexts that involve unpredictable outcomes, such as hunting. Accordingly, hunting—particularly fish-hunting—may not inherently exhibit sex-based differences.



#### ■ Data Availability

The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request. Video recordings used for behavioral analyses are not publicly available due to file size limitations and copyright considerations, but are available from the corresponding author upon reasonable request.

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■ Author contributions

A.T., T.M., and M.T. conceived the study and designed the project. A.T. analyzed behavioral data. A.T. and T.M. analyzed the dataset. A.T., T.M., E.N., K.H., G.Y., T.O., M.I., and S.I. conducted fieldwork and collected data. T.M. wrote the first draft of the manuscript. A.T., T.M., E.N., M.T., and K.T. reviewed and edited the manuscript.

#### ■Competing interests

The authors declare no conflicts of interest.

#### ■Materials & Correspondence

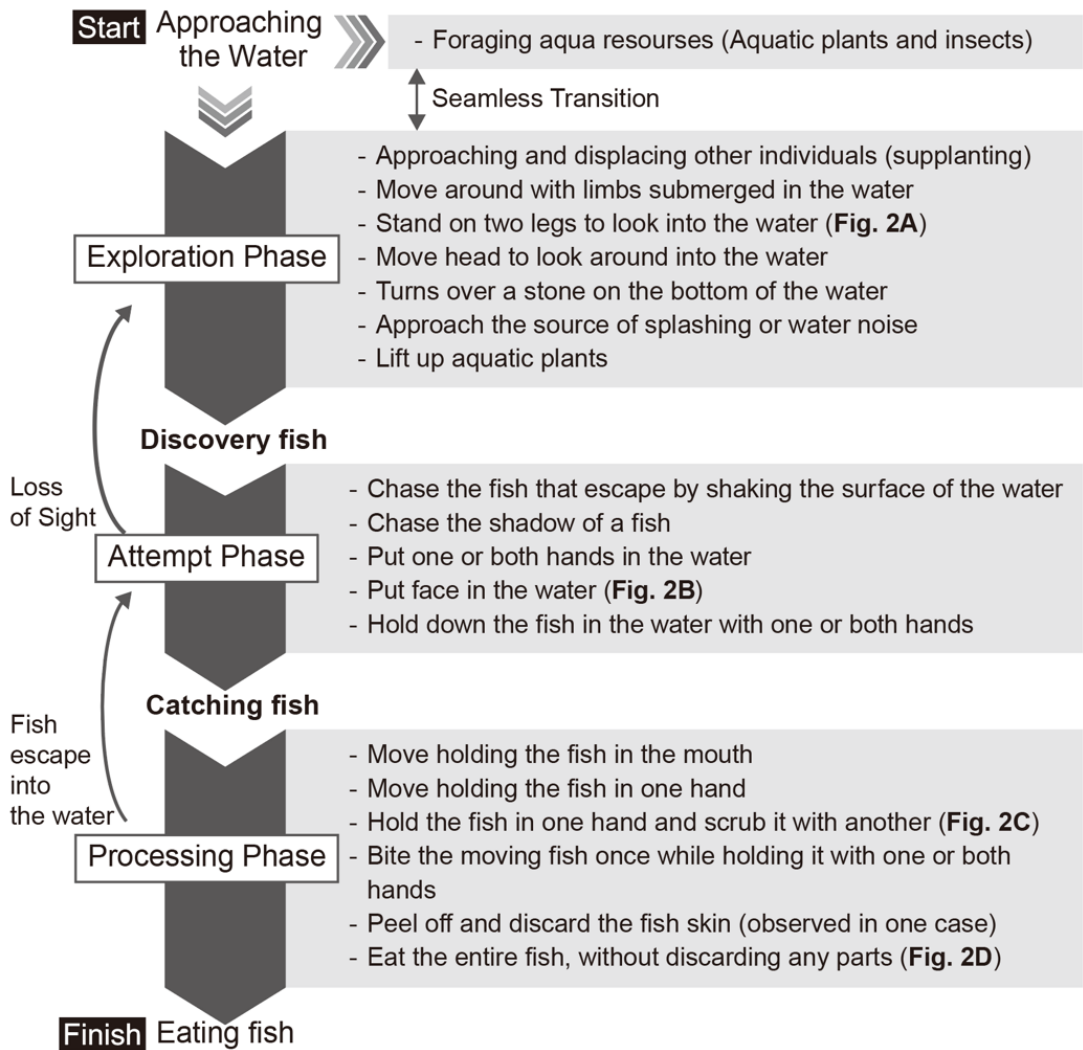
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■Figure legends

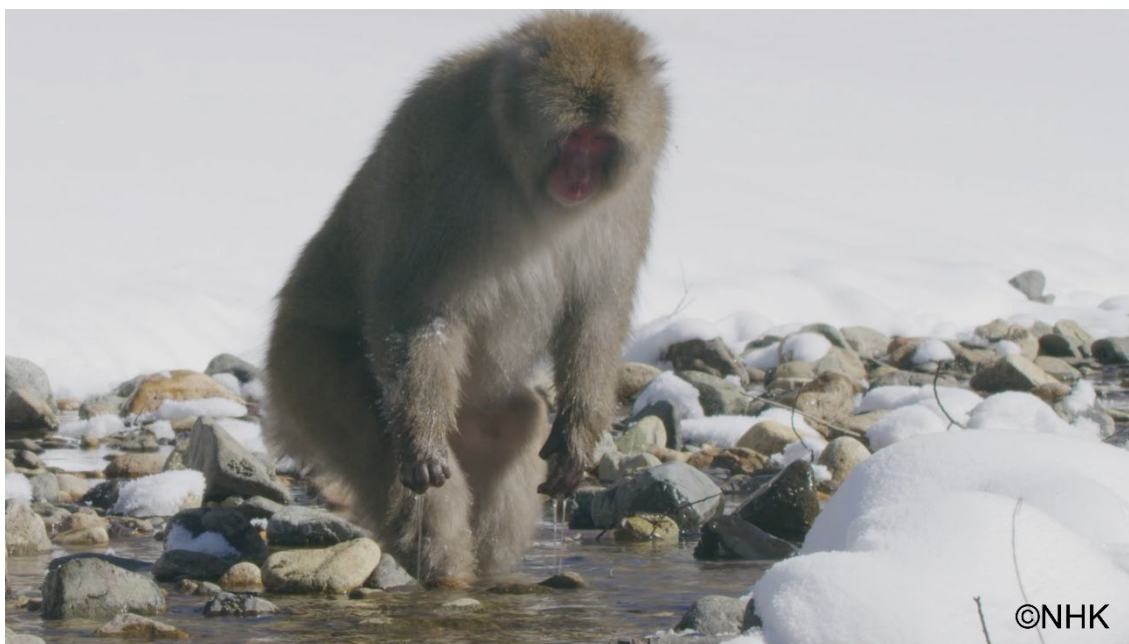
**Figure 1. Sequential phases and associated behaviors in fish-hunting by Japanese macaques**



The fish-hunting sequence comprises exploration, attempt, and processing phases. Macaques entered the exploration phase either directly or after foraging

599 aquatic plants and insects. Transitions were often seamless. Exploration involved  
600 looking into the water, turning over stones, and supplanting others. Upon  
601 detecting fish, macaques moved to the attempt phase, which included chasing,  
602 reaching into the water, or placing the face in the water. In the processing  
603 phase, fish were handled with the mouth or hands and usually consumed  
604 entirely. In rare cases, fish escaped, or the skin was peeled and discarded. The  
605 behaviors shown in Figs. 2A–2C are noted in parentheses.

**Figure 2. Representative behaviors observed during fish-hunting**



(A) An adult male inspects the water in a shallow stream during the exploration phase, standing with its hindlimbs submerged.



611 (B) An adult male places its face in the water to catch fish, a behavior  
612 characteristic of the attempt phase.

613



614 (C) An adult female holds a captured fish simultaneously in the mouth and  
615 both hands during the processing phase.

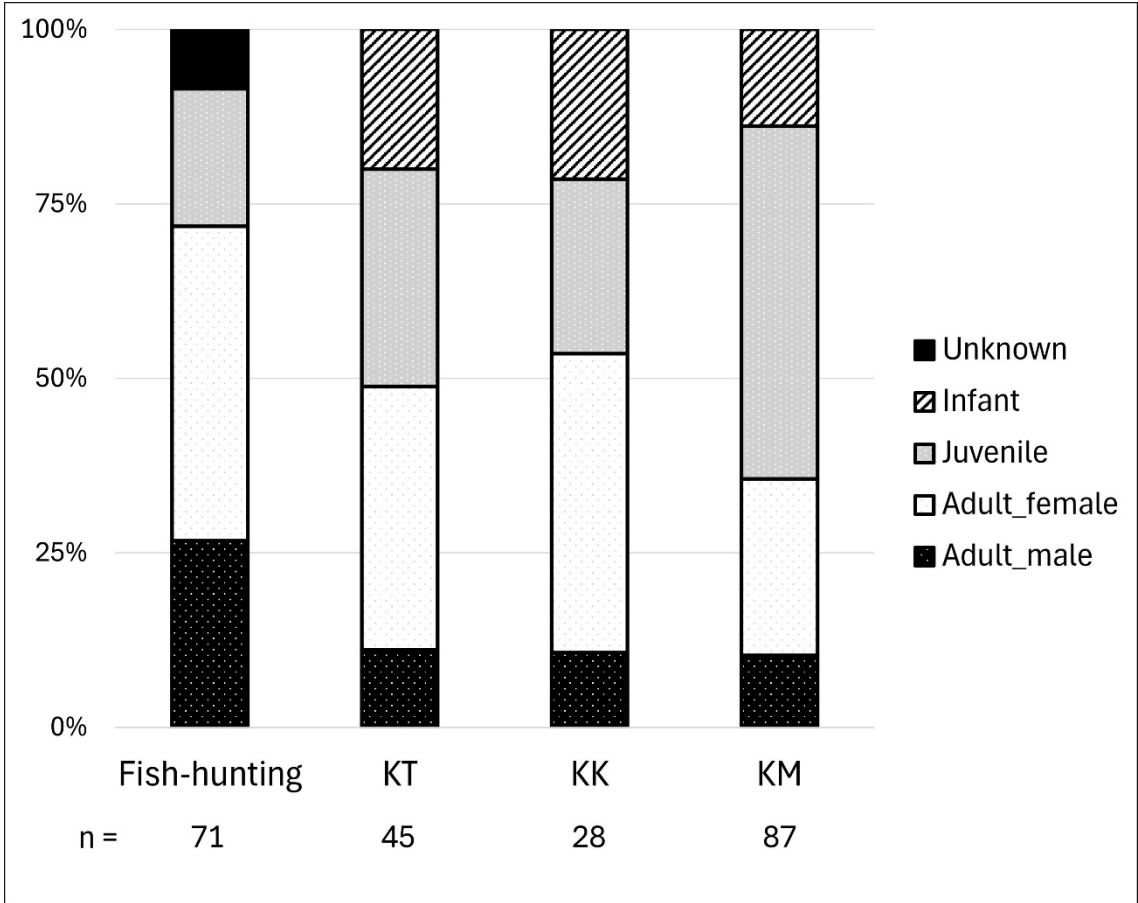
616 All images are still frames extracted from video footage filmed by NHK in

617 Kamikochi, Japan.

618



**Figure 3. Composition of sex and age classes for fish-hunting events and group members**



The left bar shows the proportion of sex and age classes in 71 documented fish-hunting events. The three right bars show the group composition of adult males, adult females, juveniles, and infants in the KT, KK, and KM groups (n = 45, 28, and 87 individuals, respectively). Individuals with an unconfirmed identity were categorized as "Unknown" in fish-hunting events.

Table 1. Fish-catching and consumption by non-human primates

Primate species	Wild or captive	Sex	Adult or young	Place	Hand catch	Tool use	Fish condition	Fish species	Reference
<i>Macaca fuscata</i>	wild	both	both	flowing river, pool	Yes	No	live	Salmonidae, <i>Rhynchocypris lagowskii steindachneri</i>	This study; Milner et al., 2021; Takenaka et al., 2022
	free-ranging, provisioned	both	both	seashore	No	No	dead	<i>Lateolabrax japonicus</i> (Asian temperate sea bass), sardins	Leca et al., 2007; Watanabe 1989
<i>Allenopithecus nigroviridis</i>	wild	*	*	pool	Yes	No	live	*	Zeeve 1985
<i>Cercopithecus neglectus</i>	wild	*	*	pool	Yes	No	live	*	Zeeve 1985
<i>Macaca fascicularis</i>	wild	female	Adult	pool or very slow river	Yes	No	live	unid. sp.(Teleostei)	Stewart et al., 2008
<i>Otolemur crassicaudatus</i>	captive	both	adult	glass	Yes	No	live	<i>Xiphophorus</i> sp.	Welker 1976
<i>Papio anubis</i>	wild	both	both	lakeshore	No	No	dead	<i>Stolothrissa tanganicae</i> (dagaa, Tanaganian sardine), <i>Boulengerio microlepis</i> (Kuhe)	Matsumoto-Oda and Collins, 2016
<i>Papio ursinus</i>	wild	both	both	pool	Yes	Yes	live	<i>Sarotherodon mossambicus</i> (tilapia), <i>Cyprinus carpio</i>	Hamilton et al., 1976; Hamilton and Tilson, 1985

								(common carp), <i>Barbus anoplus</i> (chubby head carp)	
<i>Pan paniscus</i> <sup>a</sup>	wild	*	*	pool	Yes	No	live	"mud fish," sp. unid.	Nishida 1972
<i>Pan troglodytes</i> <sup>a</sup>	wild	*	*	pool	Yes	No	live	"small fish," sp. unid.	Sugiyama and Koman, 1987
<i>Pongo pygmaeus</i>	free-ranging, rehabilitant	both	young	pool, riverbank	Yes	Yes	live	sheath catfish ( <i>Kryptopterus</i> spp., <i>Ompok</i> spp, <i>Wallago leerii</i> ), snakeheads ( <i>Channa</i> sp.)	Russon et al., 2014
<i>Sapajus apella</i>	captive	both	both	pool?*	Yes	Yes	live	*	Clarke and Mitchell, 1982; Mendes et al., 2000
<i>Tarsius bancanus</i> <sup>b</sup>	free-ranging	*	*	*	No	No	dead	unid. spp.(Actinopterygii)	Niemitz, 1979; Niemitz 1984
<i>Tarsius syrichta</i>	captive	*	*	pool	Yes	No	live	"small fish," sp. unid.	Cook, 1939

\* No description

a Information gathered from field assistants

b "when being fed a fish liked to eat the dead fish completely"