

1 **Biology, ecology, and biogeography of the enigmatic desert praying mantis *Blepharopsis***
2 ***mendica* (Insecta: Mantodea)**

3 **Zohreh Mirzaee^{1,2,3}, Marianna Simões⁴, Roberto Battiston⁵, Saber Sadeghi², Martin**
4 **Wiemers¹, Thomas Schmitt^{1,3}**

5 ¹Senckenberg German Entomological Institute, Eberswalder Str. 90, 15374 Müncheberg,
6 Germany

7 ²Biology Department, Faculty of Sciences, Shiraz University, Shiraz, Iran

8 ³Entomology and Biogeography, Institute of Biochemistry and Biology, Faculty of Science,
9 University of Potsdam, D-14476 Potsdam, Germany

10 ⁴Senckenberg Research Institute and Natural History Museum, Senckenberganlage 25, 60325,
11 Frankfurt am Main, Germany

12 ⁵Museo di Archeologia e Scienze Naturali “G. Zannato”, Montecchio Maggiore, Italy

13 Corresponding Author: Zohreh Mirzaee

14 Senckenberg German Entomological Institute, Eberswalder Str. 90, 15374
15 Müncheberg, Germany

16 Email address: zmirzaee1988@gmail.com

17 **Abstract**

18 **Background.** *Blepharopsis mendica* (Fabricius, 1775), is a large mantid species found from the Canary
19 Islands across North Africa, the Middle East, and Pakistan. Research on this species has been limited,
20 especially in Iran, despite the country's potential significance for studying its biology and distribution.
21 Adults of this species are easily recognizable by their marble-white pattern and rhomboidal leaf-like
22 pronotum. They are sit-and-wait predators that inhabit various open environments, including trees and
23 shrubs.

24 **Methods.** Field observations were conducted across various regions of the Devil's flower
25 mantis (*Blepharopsis mendica*) global distribution, with a focus on Morocco, Tunisia, and Iran.

26 Distribution data for *B. mendica* were gathered from fieldwork, museum collections, online
27 biodiversity databases, and publications, totaling 593 occurrence points. Ecological niche
28 modeling was performed using environmental data, and various models were evaluated for
29 suitability. Phylogeographic analyses involved DNA sequencing and construction of a

Kommentiert [P1]: Please do not call it “Devil's Flower Mantis”. The correct version of the vernacular name is “Devil's Flower” and the correct scientific name is *Idolomantis diabolica* (Saussure, 1869). At the end of the 19th and the beginning of the 20th century, the deimatic display of *Idolomantis* was misinterpreted as a prey-catching mechanism (see Schwarz 1996). *Blepharopsis mendica* is known as “Egyptian Mantis” or “Thistle Mantis”. Its association with “Devil's Flower” is a common misconception on the Internet.

For history of the name see: Schwarz 1996, 1997; Sommerhalder J. (2006): Die Teufelsfliegen (*Idolomantis diabolica* (Saussure, 1869) – Teil 1. Teil 2. Teil 3. Teil 4. Teil 5. Teil 6. Teil 7. Teil 8. Teil 9. Teil 10. Teil 11. Teil 12. Teil 13. Teil 14. Teil 15. Teil 16. Teil 17. Teil 18. Teil 19. Teil 20. Teil 21. Teil 22. Teil 23. Teil 24. Teil 25. Teil 26. Teil 27. Teil 28. Teil 29. Teil 30. Teil 31. Teil 32. Teil 33. Teil 34. Teil 35. Teil 36. Teil 37. Teil 38. Teil 39. Teil 40. Teil 41. Teil 42. Teil 43. Teil 44. Teil 45. Teil 46. Teil 47. Teil 48. Teil 49. Teil 50. Teil 51. Teil 52. Teil 53. Teil 54. Teil 55. Teil 56. Teil 57. Teil 58. Teil 59. Teil 60. Teil 61. Teil 62. Teil 63. Teil 64. Teil 65. Teil 66. Teil 67. Teil 68. Teil 69. Teil 70. Teil 71. Teil 72. Teil 73. Teil 74. Teil 75. Teil 76. Teil 77. Teil 78. Teil 79. Teil 80. Teil 81. Teil 82. Teil 83. Teil 84. Teil 85. Teil 86. Teil 87. Teil 88. Teil 89. Teil 90. Teil 91. Teil 92. Teil 93. Teil 94. Teil 95. Teil 96. Teil 97. Teil 98. Teil 99. Teil 100. Teil 101. Teil 102. Teil 103. Teil 104. Teil 105. Teil 106. Teil 107. Teil 108. Teil 109. Teil 110. Teil 111. Teil 112. Teil 113. Teil 114. Teil 115. Teil 116. Teil 117. Teil 118. Teil 119. Teil 120. Teil 121. Teil 122. Teil 123. Teil 124. Teil 125. Teil 126. Teil 127. Teil 128. Teil 129. Teil 130. Teil 131. Teil 132. Teil 133. Teil 134. Teil 135. Teil 136. Teil 137. Teil 138. Teil 139. Teil 140. Teil 141. Teil 142. Teil 143. Teil 144. Teil 145. Teil 146. Teil 147. Teil 148. Teil 149. Teil 150. Teil 151. Teil 152. Teil 153. Teil 154. Teil 155. Teil 156. Teil 157. Teil 158. Teil 159. Teil 160. Teil 161. Teil 162. Teil 163. Teil 164. Teil 165. Teil 166. Teil 167. Teil 168. Teil 169. Teil 170. Teil 171. Teil 172. Teil 173. Teil 174. Teil 175. Teil 176. Teil 177. Teil 178. Teil 179. Teil 180. Teil 181. Teil 182. Teil 183. Teil 184. Teil 185. Teil 186. Teil 187. Teil 188. Teil 189. Teil 190. Teil 191. Teil 192. Teil 193. Teil 194. Teil 195. Teil 196. Teil 197. Teil 198. Teil 199. Teil 200. Teil 201. Teil 202. Teil 203. Teil 204. Teil 205. Teil 206. Teil 207. Teil 208. Teil 209. Teil 210. Teil 211. Teil 212. Teil 213. Teil 214. Teil 215. Teil 216. Teil 217. Teil 218. Teil 219. Teil 220. Teil 221. Teil 222. Teil 223. Teil 224. Teil 225. Teil 226. Teil 227. Teil 228. Teil 229. Teil 230. Teil 231. Teil 232. Teil 233. Teil 234. Teil 235. Teil 236. Teil 237. Teil 238. Teil 239. Teil 240. Teil 241. Teil 242. Teil 243. Teil 244. Teil 245. Teil 246. Teil 247. Teil 248. Teil 249. Teil 250. Teil 251. Teil 252. Teil 253. Teil 254. Teil 255. Teil 256. Teil 257. Teil 258. Teil 259. Teil 260. Teil 261. Teil 262. Teil 263. Teil 264. Teil 265. Teil 266. Teil 267. Teil 268. Teil 269. Teil 270. Teil 271. Teil 272. Teil 273. Teil 274. Teil 275. Teil 276. Teil 277. Teil 278. Teil 279. Teil 280. Teil 281. Teil 282. Teil 283. Teil 284. Teil 285. Teil 286. Teil 287. Teil 288. Teil 289. Teil 290. Teil 291. Teil 292. Teil 293. Teil 294. Teil 295. Teil 296. Teil 297. Teil 298. Teil 299. Teil 300. Teil 301. Teil 302. Teil 303. Teil 304. Teil 305. Teil 306. Teil 307. Teil 308. Teil 309. Teil 310. Teil 311. Teil 312. Teil 313. Teil 314. Teil 315. Teil 316. Teil 317. Teil 318. Teil 319. Teil 320. Teil 321. Teil 322. Teil 323. Teil 324. Teil 325. Teil 326. Teil 327. Teil 328. Teil 329. Teil 330. Teil 331. Teil 332. Teil 333. Teil 334. Teil 335. Teil 336. Teil 337. Teil 338. Teil 339. Teil 340. Teil 341. Teil 342. Teil 343. Teil 344. Teil 345. Teil 346. Teil 347. Teil 348. Teil 349. Teil 350. Teil 351. Teil 352. Teil 353. Teil 354. Teil 355. Teil 356. Teil 357. Teil 358. Teil 359. Teil 360. Teil 361. Teil 362. Teil 363. Teil 364. Teil 365. Teil 366. Teil 367. Teil 368. Teil 369. Teil 370. Teil 371. Teil 372. Teil 373. Teil 374. Teil 375. Teil 376. Teil 377. Teil 378. Teil 379. Teil 380. Teil 381. Teil 382. Teil 383. Teil 384. Teil 385. Teil 386. Teil 387. Teil 388. Teil 389. Teil 390. Teil 391. Teil 392. Teil 393. Teil 394. Teil 395. Teil 396. Teil 397. Teil 398. Teil 399. Teil 400. Teil 401. Teil 402. Teil 403. Teil 404. Teil 405. Teil 406. Teil 407. Teil 408. Teil 409. Teil 410. Teil 411. Teil 412. Teil 413. Teil 414. Teil 415. Teil 416. Teil 417. Teil 418. Teil 419. Teil 420. Teil 421. Teil 422. Teil 423. Teil 424. Teil 425. Teil 426. Teil 427. Teil 428. Teil 429. Teil 430. Teil 431. Teil 432. Teil 433. Teil 434. Teil 435. Teil 436. Teil 437. Teil 438. Teil 439. Teil 440. Teil 441. Teil 442. Teil 443. Teil 444. Teil 445. Teil 446. Teil 447. Teil 448. Teil 449. Teil 450. Teil 451. Teil 452. Teil 453. Teil 454. Teil 455. Teil 456. Teil 457. Teil 458. Teil 459. Teil 460. Teil 461. Teil 462. Teil 463. Teil 464. Teil 465. Teil 466. Teil 467. Teil 468. Teil 469. Teil 470. Teil 471. Teil 472. Teil 473. Teil 474. Teil 475. Teil 476. Teil 477. Teil 478. Teil 479. Teil 480. Teil 481. Teil 482. Teil 483. Teil 484. Teil 485. Teil 486. Teil 487. Teil 488. Teil 489. Teil 490. Teil 491. Teil 492. Teil 493. Teil 494. Teil 495. Teil 496. Teil 497. Teil 498. Teil 499. Teil 500. Teil 501. Teil 502. Teil 503. Teil 504. Teil 505. Teil 506. Teil 507. Teil 508. Teil 509. Teil 510. Teil 511. Teil 512. Teil 513. Teil 514. Teil 515. Teil 516. Teil 517. Teil 518. Teil 519. Teil 520. Teil 521. Teil 522. Teil 523. Teil 524. Teil 525. Teil 526. Teil 527. Teil 528. Teil 529. Teil 530. Teil 531. Teil 532. Teil 533. Teil 534. Teil 535. Teil 536. Teil 537. Teil 538. Teil 539. Teil 540. Teil 541. Teil 542. Teil 543. Teil 544. Teil 545. Teil 546. Teil 547. Teil 548. Teil 549. Teil 550. Teil 551. Teil 552. Teil 553. Teil 554. Teil 555. Teil 556. Teil 557. Teil 558. Teil 559. Teil 560. Teil 561. Teil 562. Teil 563. Teil 564. Teil 565. Teil 566. Teil 567. Teil 568. Teil 569. Teil 570. Teil 571. Teil 572. Teil 573. Teil 574. Teil 575. Teil 576. Teil 577. Teil 578. Teil 579. Teil 580. Teil 581. Teil 582. Teil 583. Teil 584. Teil 585. Teil 586. Teil 587. Teil 588. Teil 589. Teil 590. Teil 591. Teil 592. Teil 593. Teil 594. Teil 595. Teil 596. Teil 597. Teil 598. Teil 599. Teil 600. Teil 601. Teil 602. Teil 603. Teil 604. Teil 605. Teil 606. Teil 607. Teil 608. Teil 609. Teil 610. Teil 611. Teil 612. Teil 613. Teil 614. Teil 615. Teil 616. Teil 617. Teil 618. Teil 619. Teil 620. Teil 621. Teil 622. Teil 623. Teil 624. Teil 625. Teil 626. Teil 627. Teil 628. Teil 629. Teil 630. Teil 631. Teil 632. Teil 633. Teil 634. Teil 635. Teil 636. Teil 637. Teil 638. Teil 639. Teil 640. Teil 641. Teil 642. Teil 643. Teil 644. Teil 645. Teil 646. Teil 647. Teil 648. Teil 649. Teil 650. Teil 651. Teil 652. Teil 653. Teil 654. Teil 655. Teil 656. Teil 657. Teil 658. Teil 659. Teil 660. Teil 661. Teil 662. Teil 663. Teil 664. Teil 665. Teil 666. Teil 667. Teil 668. Teil 669. Teil 670. Teil 671. Teil 672. Teil 673. Teil 674. Teil 675. Teil 676. Teil 677. Teil 678. Teil 679. Teil 680. Teil 681. Teil 682. Teil 683. Teil 684. Teil 685. Teil 686. Teil 687. Teil 688. Teil 689. Teil 690. Teil 691. Teil 692. Teil 693. Teil 694. Teil 695. Teil 696. Teil 697. Teil 698. Teil 699. Teil 700. Teil 701. Teil 702. Teil 703. Teil 704. Teil 705. Teil 706. Teil 707. Teil 708. Teil 709. Teil 710. Teil 711. Teil 712. Teil 713. Teil 714. Teil 715. Teil 716. Teil 717. Teil 718. Teil 719. Teil 720. Teil 721. Teil 722. Teil 723. Teil 724. Teil 725. Teil 726. Teil 727. Teil 728. Teil 729. Teil 730. Teil 731. Teil 732. Teil 733. Teil 734. Teil 735. Teil 736. Teil 737. Teil 738. Teil 739. Teil 740. Teil 741. Teil 742. Teil 743. Teil 744. Teil 745. Teil 746. Teil 747. Teil 748. Teil 749. Teil 750. Teil 751. Teil 752. Teil 753. Teil 754. Teil 755. Teil 756. Teil 757. Teil 758. Teil 759. Teil 760. Teil 761. Teil 762. Teil 763. Teil 764. Teil 765. Teil 766. Teil 767. Teil 768. Teil 769. Teil 770. Teil 771. Teil 772. Teil 773. Teil 774. Teil 775. Teil 776. Teil 777. Teil 778. Teil 779. Teil 780. Teil 781. Teil 782. Teil 783. Teil 784. Teil 785. Teil 786. Teil 787. Teil 788. Teil 789. Teil 790. Teil 791. Teil 792. Teil 793. Teil 794. Teil 795. Teil 796. Teil 797. Teil 798. Teil 799. Teil 800. Teil 801. Teil 802. Teil 803. Teil 804. Teil 805. Teil 806. Teil 807. Teil 808. Teil 809. Teil 810. Teil 811. Teil 812. Teil 813. Teil 814. Teil 815. Teil 816. Teil 817. Teil 818. Teil 819. Teil 820. Teil 821. Teil 822. Teil 823. Teil 824. Teil 825. Teil 826. Teil 827. Teil 828. Teil 829. Teil 830. Teil 831. Teil 832. Teil 833. Teil 834. Teil 835. Teil 836. Teil 837. Teil 838. Teil 839. Teil 840. Teil 841. Teil 842. Teil 843. Teil 844. Teil 845. Teil 846. Teil 847. Teil 848. Teil 849. Teil 850. Teil 851. Teil 852. Teil 853. Teil 854. Teil 855. Teil 856. Teil 857. Teil 858. Teil 859. Teil 860. Teil 861. Teil 862. Teil 863. Teil 864. Teil 865. Teil 866. Teil 867. Teil 868. Teil 869. Teil 870. Teil 871. Teil 872. Teil 873. Teil 874. Teil 875. Teil 876. Teil 877. Teil 878. Teil 879. Teil 880. Teil 881. Teil 882. Teil 883. Teil 884. Teil 885. Teil 886. Teil 887. Teil 888. Teil 889. Teil 890. Teil 891. Teil 892. Teil 893. Teil 894. Teil 895. Teil 896. Teil 897. Teil 898. Teil 899. Teil 900. Teil 901. Teil 902. Teil 903. Teil 904. Teil 905. Teil 906. Teil 907. Teil 908. Teil 909. Teil 910. Teil 911. Teil 912. Teil 913. Teil 914. Teil 915. Teil 916. Teil 917. Teil 918. Teil 919. Teil 920. Teil 921. Teil 922. Teil 923. Teil 924. Teil 925. Teil 926. Teil 927. Teil 928. Teil 929. Teil 930. Teil 931. Teil 932. Teil 933. Teil 934. Teil 935. Teil 936. Teil 937. Teil 938. Teil 939. Teil 940. Teil 941. Teil 942. Teil 943. Teil 944. Teil 945. Teil 946. Teil 947. Teil 948. Teil 949. Teil 950. Teil 951. Teil 952. Teil 953. Teil 954. Teil 955. Teil 956. Teil 957. Teil 958. Teil 959. Teil 960. Teil 961. Teil 962. Teil 963. Teil 964. Teil 965. Teil 966. Teil 967. Teil 968. Teil 969. Teil 970. Teil 971. Teil 972. Teil 973. Teil 974. Teil 975. Teil 976. Teil 977. Teil 978. Teil 979. Teil 980. Teil 981. Teil 982. Teil 983. Teil 984. Teil 985. Teil 986. Teil 987. Teil 988. Teil 989. Teil 990. Teil 991. Teil 992. Teil 993. Teil 994. Teil 995. Teil 996. Teil 997. Teil 998. Teil 999. Teil 1000. Teil 1001. Teil 1002. Teil 1003. Teil 1004. Teil 1005. Teil 1006. Teil 1007. Teil 1008. Teil 1009. Teil 1010. Teil 1011. Teil 1012. Teil 1013. Teil 1014. Teil 1015. Teil 1016. Teil 1017. Teil 1018. Teil 1019. Teil 1020. Teil 1021. Teil 1022. Teil 1023. Teil 1024. Teil 1025. Teil 1026. Teil 1027. Teil 1028. Teil 1029. Teil 1030. Teil 1031. Teil 1032. Teil 1033. Teil 1034. Teil 1035. Teil 1036. Teil 1037. Teil 1038. Teil 1039. Teil 1040. Teil 1041. Teil 1042. Teil 1043. Teil 1044. Teil 1045. Teil 1046. Teil 1047. Teil 1048. Teil 1049. Teil 1050. Teil 1051. Teil 1052. Teil 1053. Teil 1054. Teil 1055. Teil 1056. Teil 1057. Teil 1058. Teil 1059. Teil 1060. Teil 1061. Teil 1062. Teil 1063. Teil 1064. Teil 1065. Teil 1066. Teil 1067. Teil 1068. Teil 1069. Teil 1070. Teil 1071. Teil 1072. Teil 1073. Teil 1074. Teil 1075. Teil 1076. Teil 1077. Teil 1078. Teil 1079. Teil 1080. Teil 1081. Teil 1082. Teil 1083. Teil 1084. Teil 1085. Teil 1086. Teil 1087. Teil 1088. Teil 1089. Teil 1090. Teil 1091. Teil 1092. Teil 1093. Teil 1094. Teil 1095. Teil 1096. Teil 1097. Teil 1098. Teil 1099. Teil 1100. Teil 1101. Teil 1102. Teil 1103. Teil 1104. Teil 1105. Teil 1106. Teil 1107. Teil 1108. Teil 1109. Teil 1110. Teil 1111. Teil 1112. Teil 1113. Teil 1114. Teil 1115. Teil 1116. Teil 1117. Teil 1118. Teil 1119. Teil 1120. Teil 1121. Teil 1122. Teil 1123. Teil 1124. Teil 1125. Teil 1126. Teil 1127. Teil 1128. Teil 1129. Teil 1130. Teil 1131. Teil 1132. Teil 1133. Teil 1134. Teil 1135. Teil 1136. Teil 1137. Teil 1138. Teil 1139. Teil 1140. Teil 1141. Teil 1142. Teil 1143. Teil 1144. Teil 1145. Teil 1146. Teil 1147. Teil 1148. Teil 1149. Teil 1150. Teil 1151. Teil 1152. Teil 1153. Teil 1154. Teil 1155. Teil 1156. Teil 1157. Teil 1158. Teil 1159. Teil 1160. Teil 1161. Teil 1162. Teil 1163. Teil 1164. Teil 1165. Teil 1166. Teil 1167. Teil 1168. Teil 1169. Teil 1170. Teil 1171. Teil 1172. Teil 1173. Teil 1174. Teil 1175. Teil 1176. Teil 1177. Teil 1178. Teil 1179. Teil 1180. Teil 1181. Teil 1182. Teil 1183. Teil 1184. Teil 1185. Teil 1186. Teil 1187. Teil 1188. Teil 1189. Teil 1190. Teil 1191. Teil 1192. Teil 1193. Teil 1194. Teil 1195. Teil 1196. Teil 1197. Teil 1198. Teil 1199. Teil 1200. Teil 1201. Teil 1202. Teil 1203. Teil 1204. Teil 1205. Teil 1206. Teil 1207. Teil 1208. Teil 1209. Teil 1210. Teil 1211. Teil 1212. Teil 1213. Teil 1214. Teil 1215. Teil 1216. Teil 1217. Teil 1218. Teil 1219. Teil 1220. Teil 1221. Teil 1222. Teil 1223. Teil 1224. Teil 1225. Teil 1226. Teil 1227. Teil 1228. Teil 1229. Teil 1230. Teil 1231. Teil 1232. Teil 1233. Teil 1234. Teil 1235. Teil 1236. Teil 1237. Teil 1238. Teil 1239. Teil 1240. Teil 1241. Teil 1242. Teil 1243. Teil 1244. Teil 1245. Teil 1246. Teil 1247. Teil 1248. Teil 1249. Teil 1250. Teil 1251. Teil 1252. Teil 1253. Teil 1254. Teil 1255. Teil 1256. Teil 1257. Teil 1258. Teil 1259. Teil 1260. Teil 1261. Teil 1262. Teil 1263. Teil 1264. Teil 1265. Teil 1266. Teil 1267. Teil 1268. Teil 1269. Teil 1270. Teil 1271. Teil 1272. Teil 1273. Teil 1274. Teil 1275. Teil 1276. Teil 1277. Teil 1278. Teil 1279. Teil 1280. Teil 1281. Teil 1282. Teil 1283. Teil 1284. Teil 1285. Teil 1286. Teil 1287. Teil 1288. Teil 1289. Teil 1290. Teil 1291. Teil 1292. Teil 1293. Teil 1294. Teil 1295. Teil 1296. Teil 1297. Teil 1298. Teil 1299. Teil 1300. Teil 1301. Teil 1302. Teil 1303. Teil 1304. Teil 1305. Teil 1306. Teil 1307. Teil 1308. Teil 1309. Teil 1310. Teil 1311. Teil 1312. Teil 1313. Teil 1314. Teil 1315. Teil 1316. Teil 1317. Teil 1318. Teil 1319. Teil 1320. Teil 1321. Teil 1322. Teil 1323. Teil 1324. Teil 1325. Teil 1326. Teil 1327. Teil 1328. Teil 1329. Teil 1330. Teil 1331. Teil 1332. Teil 1333. Teil 1334. Teil 1335. Teil 1336. Teil 1337. Teil 1338. Teil 1339. Teil 1340. Teil 1341. Teil 1342. Teil 1343. Teil 1344. Teil 1345. Teil 1346. Teil 1347. Teil 1348. Teil 1349. Teil 1350. Teil 1351. Teil 1352. Teil 1353. Teil 1354. Teil 1355. Teil 1356. Teil 1357. Teil 1358. Teil 1359. Teil 1360. Teil 1361. Teil 1362. Teil 1363. Teil 1364. Teil 1365. Teil 1366. Teil 1367. Teil 1368. Teil 1369. Teil 1370. Teil 1371. Teil 1372. Teil 1373. Teil 1374. Teil 1375. Teil 1376. Teil 1377. Teil 1378. Teil 1379. Teil 1380. Teil 1381. Teil 1382. Teil 1383. Teil 1384. Teil 1385. Teil 1386. Teil 1387. Teil 1388. Teil 1389. Teil 1390. Teil 1391. Teil 1392. Teil 1393. Teil 1394. Teil 1395. Teil 1396. Teil 1397. Teil 1398. Teil 1399. Teil 1400. Teil 1401. Teil 1402. Teil 1403. Teil 1404. Teil 1405. Teil 1406. Teil 1407. Teil 1408. Teil 1409. Teil 1410. Teil 1411. Teil 1412. Teil 1413. Teil 1414. Teil 1415. Teil 1416. Teil 1417. Teil 1418. Teil 1419. Teil 1420. Teil 1421. Teil 1422. Teil 1423. Teil 1424. Teil 1425. Teil 1426. Teil 1427. Teil 1428. Teil 1429. Teil 1430. Teil 1431. Teil 1432. Teil 1433. Teil 1434. Teil 1435. Teil 1436. Teil 1437. Teil 1438. Teil 1439. Teil 1440. Teil 1441. Teil 1442. Teil 1443. Teil 1444. Teil 1445. Teil 1446. Teil 1447. Teil 1448. Teil 1449. Teil 1450. Teil 1451. Teil 1452. Teil 1453. Teil 1454. Teil 1455. Teil 1456. Teil 1457. Teil 1458. Teil 1459. Teil 1460. Teil 1461. Teil 1462. Teil 1463. Teil 1464. Teil 1465. Teil 1466. Teil 1467. Teil 1468. Teil 1469. Teil 1470. Teil 1471. Teil 1472. Teil 1473. Teil 1474. Teil 1475. Teil 1476. Teil 1477. Teil 1478. Teil 1479. Teil 1480. Teil 1481. Teil 1482. Teil 1483. Teil 1484. Teil 1485. Teil 1486. Teil 1487. Teil 1488. Teil 1489. Teil 1490. Teil 1491. Teil 1492. Teil 1493. Teil 1494. Teil 1495. Teil 1496. Teil 1497. Teil 1498. Teil 1499. Teil 1500. Teil 1501. Teil 1502. Teil 1503. Teil 1504. Teil 1505. Teil 1506. Teil 1507. Teil 1508. Teil 1509. Teil 1510. Teil 1511. Teil 1512. Teil 1513. Teil 1514. Teil 1515. Teil 1516. Teil 1517. Teil 1518. Teil 1519. Teil 1520. Teil 1521. Teil 1522. Teil 1523. Teil 1524. Teil 1525. Teil 1526. Teil 1527. Teil 1528. Teil 1529. Teil 1530. Teil 1531. Teil 1532. Teil 1533. Teil 1534. Teil 1535. Teil 1536. Teil 1537. Teil 1538. Teil 1539. Teil 1540. Teil 1541. Teil 1542. Teil 1543. Teil 1544. Teil 1545. Teil 1546. Teil 1547. Teil 1548. Teil 1549. Teil 1550. Teil 1551. Teil 1552. Teil 1553. Teil 1554. Teil 1555. Teil 1556. Teil 1557. Teil 1558. Teil 1559. Teil 1560. Teil 1561. Teil 1562. Teil 1563. Teil 1564. Teil 1565. Teil 1566. Teil 1567. Teil 1568. Teil 1569. Teil 1570. Teil 1571. Teil 1572. Teil 1573. Teil 1574. Teil 1575. Teil 1576. Teil 1577. Teil 1578. Teil 1579. Teil 1580. Teil 1581. Teil 1582. Teil 1583. Teil 1584. Teil 1585. Teil 1586. Teil 1587. Teil 1588. Teil 1589. Teil 1590. Teil 1591. Teil 1592. Teil 1593. Teil 1594. Teil 1595. Teil 1596. Teil 1597. Teil 1598. Teil 1599. Teil 1600. Teil 1601. Teil 1602. Teil 1603. Teil 1604. Teil 1605. Teil 1606. Teil 1607. Teil 1608. Teil 1609. Teil 1610. Teil 1611. Teil 1612. Teil 1613. Teil 1614. Teil 1615. Teil 1616. Teil 1617. Teil 1618. Teil 1619. Teil 1620. Teil 1621. Teil 1622. Teil 1623. Teil 1624. Teil 1625. Teil 1626. Teil 1627. Teil 1628. Teil 1629. Teil 1630. Teil 1631. Teil 1632. Teil 1633. Teil 1634. Teil 1635. Teil 1636. Teil 1637. Teil 1638. Teil 1639. Teil 1640. Teil 1641. Teil 1642. Teil 1643. Teil 1644. Teil 1645. Teil 1646. Teil 1647. Teil 1648. Teil 1649. Teil 1650. Teil 1651. Teil 1652. Teil 1653. Teil 1654. Teil 1655. Teil 1656. Teil 1657. Teil 1658. Teil 1659. Teil 1660. Teil 1661. Teil 1662. Teil 1663. Teil 1664. Teil 1665. Teil 1666. Teil 1667. Teil 1668. Teil 1669. Teil 1670. Teil 1671. Teil 1672. Teil 1673. Teil 1674. Teil 1675. Teil 1676. Teil 1677. Teil 1678. Teil 1679. Teil 1680. Teil 1681. Teil 1682. Teil 1683. Teil 1684. Teil 1685. Teil 1686. Teil 1687. Teil 1688. Teil 1689. Teil 1690. Teil 1691. Teil 1692. Teil 1693. Teil 1694. Teil 1695. Teil 1696. Teil 1697. Teil 1698. Teil 1699. Teil 1700. Teil 1701. Teil 1702. Teil 1703. Teil 1704. Teil 1705. Teil 1706. Teil 1707. Teil 1708. Teil 1709. Teil 1710. Teil 1711. Teil 1712. Teil 1713. Teil 1714. Teil 1715. Teil 1716. Teil 1717. Teil 1718. Teil 1719. Teil 1720. Teil 1721. Teil 172

haplotype network to examine genetic relationships between populations. Divergence time estimation and biogeographical range expansion models were applied to explore historical distribution shifts of the species across different regions. The study provided comprehensive insights into the biology, distribution, and genetic history of *B. mendica*.

Results. We provide information on the life cycle, ootheca, defense behavior, habitat, and biogeography of ~~the Devil's flower mantis~~, *Blepharopsis mendica*. This mantid is an overwintering univoltine species with nymphs emerging in summer and becoming adults in spring. In the wild, females start oviposition in April and can lay their first ootheca within a week after mating. The species is distributed from the Canary Islands to Pakistan in the dry belt. Thus, its distribution is associated with xeric areas or savanna-like habitats. Phylogeographic analyses revealed three major genetic lineages, (i) in the Maghreb, (ii) from Egypt via Arabia to Iran (with internal substructures), and (iii) likely in Pakistan; the estimated onset of differentiation into these lineages is of Pleistocene age. Defense behavior involves flying away or extending wings broadly and lifting forelegs. Performing laboratory breeding, we documented life cycle and color changes from first instar to adulthood. Due to overwintering, the last larval instar needs considerably longer than the others. At 25 °C (± 2), average adult life span was 118 days (± 6 SD) for females (range: 100–124) and 46 days (± 5 SD) for males (range: 39–55), with a significant difference among sexes. On average, oothecae contained 32.3 eggs (± 10.1 SD) and the mean incubation period was 36.8 days (± 2.9 SD). We did not find evidence of parthenogenesis. In general, the biology of *B. mendica* shows a variety of adaptations to its often extreme and little predictable type of habitat.

Keywords: ~~Devil's flower mantis~~, life history, ootheca, mantid, adaptation, extreme habitats

Introduction

Praying mantids occupy an important ecological niche, playing vital roles as predators. These creatures are renowned for their distinctive appearance and predatory prowess, wielding their razor-sharp forelegs with precision to capture and subdue a wide array of prey, including other insects, small fauna, and even their own kind. In this intricate web of life, their presence underscores the delicate balance and the indispensable role of these fierce predators in maintaining the equilibrium of insect populations within many of the world's diverse ecosystems.

Kommentiert [P2]: More like desert species is absent from true savanna.

Kommentiert [P3]: The legs are not used for cutting. The spines increase friction, so that the prey does not escape. In some species or situations they actually cut.

Kommentiert [P4]: Citation needed.

61 The color changes of different stages of mantids also provide insights into their ecology and
62 behavior. For example, coloration may play a role in camouflage, mate selection, or predator
63 avoidance, and understanding these factors can help us to better understand the role that these
64 species play in their ecosystems (Battiston & Fontana 2010).

Kommentiert [P5]: Please provide

65 One rather spectacular mantid species is ~~the Devil's flower mantis~~ *Blepharopsis mendica*
66 (Fabricius, 1775). This large species is found from the Canary Islands throughout North Africa
67 and the Middle East to Pakistan (Battiston *et al.* 2010). Adults can be distinguished by their
68 marble-white pattern all over their bodies and the rhomboidal leaf-like shape of their pronotum.
69 This mantid, a sit-and-wait predator, inhabits open areas where it lives in trees as well as in
70 green and dried shrubs. It exhibits exceptional camouflage with its cryptic shape, color, and
71 behavior (Fig. 1), making it difficult to spot in its natural habitat (Battiston *et al.* 2010).

Kommentiert [P6]: Is this confirmed
arbusculous records.

72 Although *B. mendica* is a fascinating mantid, only two relatively old studies (i.e., Korsakoff
73 1934, 1935) dealt in more detail with the species' life cycle, biology, and other ecological
74 aspects, while the more recent publications mostly address its distribution or are only
75 presenting new faunistic records (Ehrmann, 2011; Caesar *et al.* 2015; Panhwar *et al.* 2020;
76 Nasser *et al.* 2021). In particular, for Iran, there are practically no studies concerning the
77 biology and distribution of *B. mendica*, and only records of this species from some parts of the
78 country (Lorestan and Fars provinces) have been published so far (Mirzaee & Sadeghi 2019,
79 2021a). However, Iran with its strikingly diverse array of ecosystems and hence high diversity
80 of (often endemic) insect species (cf. Zehzad *et al.* 2002) is a particularly important region for
81 the study of *B. mendica*, primarily owing to its geographically extended arid and semi-arid
82 landscapes, often characterized by scrub vegetation, the ecosystems where this species
83 typically thrives.

Kommentiert [P7]: While the pictures
species, the good camouflage does not
authors should search for a better photo
is photographed from some distance.
should be no problem. Most photographs
for scientific purposes.

84 Here, we provide detailed information regarding the color change of *B. mendica* along its
85 development under optimal laboratory conditions, its biology, life cycle, and behavior.
86 Defensive behaviors of individuals in the wild are also documented and discussed. New data
87 on the distribution of the species across Iran, where the species still is rather poorly studied, is
88 presented together with additional information on its life history in the wild. These data in
89 conclusion allow a more comprehensive understanding of the species' biology including its life
90 history, ecology, evolution, distribution, and historical biogeography.

Kommentiert [P8]: This study also
action, by synonymizing *B. mendica* m
with the nominate subspecies.

91 Materials and methods

92 Collecting and observation in the wild

Field observations have been done along the global distribution of this species to contextualize the data in a wider perspective. Wild specimens were observed and documented in three focal points of the global distribution of this species: western habitats in Morocco, central habitats in Tunisia, and eastern habitats in Iran. Individuals of *B. mendica* from nine regions in five different provinces of Iran (Lamerd, Fasa, Shiraz, Fars province; Jam, Soroo, Tombak, Bushehr province; Khomeini Shahr, Isfahan province; Abadan, Khozestan province; Eshkanan, Hormozgan province) were collected by the first author during field surveys from 2019 to 2021. The presence of individuals and their defense behavior were observed and photographed within natural habitats. Three oothecae of this species were collected from branches of trees or bushes in Darab, Fars Province, and Jam, Bushehr Province, during June and July 2020 by the first author, but they were empty and already hatched at the time of collecting. Species and ootheca identification were carried out by the first author (Z.M.) following Battiston *et al.* (2010). All materials collected during this survey are preserved in the following collections: Zohreh Mirzaee private collection, Müncheberg, Germany (ZMPC); Zoological Museum of Shiraz University, Shiraz, Iran (ZM-CBSU); and Mantodea collection of Senckenberg German Entomological Institute, Müncheberg, Germany (SDEI).

Rearing and lab condition

From two adult individuals collected from xeric shrublands of Bushehr province (27° 50' 37.35" N, 52° 03' 51.92" E), one female laid one ootheca, which was kept in a glass jar (15 × 15 × 10 cm) at room temperature (25–27 °C). The relative air humidity (RH) was maintained at 40–45 % with water misted on a regular basis. A digital terrarium hygrometer (HTC2) (Dongguan City, China) was used to measure RH.

The hatched nymphs were kept in separate glass jars (6 × 6 × 4 cm) during the first and second instar, thereafter transferred to bigger jars (12 × 12 × 10 cm). The jars containing the nymphs were maintained at 33–35 °C. One stick was placed in each jar to assist molting. Ventilation was enabled by three holes (2 mm in diameter each) in the lid of the jars. During the first and second instar, nymphs were fed with fruit flies (*Drosophila melanogaster* Meigen, 1830), two to three individuals per nymph every three days. Later instars were fed with living mealworm larvae (*Tenebrio molitor* Linnaeus, 1758), small living grasshoppers (*Calliptamus* spec.), moths (mostly *Eupithecia* spec. and *Leucania* spec.) and house flies (*Musca domestica* Linnaeus, 1758) twice a week.

All jars were checked daily. We recorded all information regarding the dates of molting and number of molts. To prevent contamination or disturbance, we removed all unfinished or dead prey. The sex of each individual was noted after the last molt. The adults were used for further breeding, testing different conditions (i.e., mated, not mated).

Data analyses of breeding

We calculated the mean number of days (with their standard deviations) between molts and adulthood (based on nymphs reaching the adult phase), separately for males and females. To assess the difference in mean adult longevity between males and females, a two-sample t-test was conducted. The t-test is appropriate for comparing the means of two independent groups. Statistical analysis was performed using RStudio 3.6.3 (R Core Team, 2021) with the base R package. Oothecae resulting from the first generation bred in captivity were measured, and the numbers of egg chambers inside fertilized and unfertilized oothecae were counted. Based on descriptions provided by Brannoch *et al.* (2017), the length, width, and height of each ootheca were assessed. To count the number of eggs per ootheca, they were dissected along their length and examined under a LEICA M205 C binocular microscope. The ootheca parameters were measured as shown in Figures 2a and b. A digital camera, Canon EOS 700D, was used to take pictures.

Distribution data

Fieldwork, museum collections, online biodiversity databases, and publications were used to collect distributional data. In total, 63 records were obtained from various districts of Iran over a seven-year survey period of the first author (2015–2021); 272 records were obtained from museum collections, including those at the State Museum of Natural History Karlsruhe, Germany (SMNK), the Zoological Research Museum Alexander Koenig, Germany (ZFMK), (all museum specimens were identified by the mantid specialist R. Ehrmann); 28 records were obtained from the Global Biodiversity Information Facility (GBIF; <https://doi.org/10.15468/dl.y25v89>), 140 from iNaturalist, including only specimens with pictures that allowed accurate species identification (confirmed by ZM); and 90 additional records from Naseer *et al.* (2021). In total, we obtained 593 occurrence points, which were used to generate a distribution map in QGIS v. 3.22 (<https://qgis.org/en/site/>). Google Earth v. 9.174.0.2 (<https://earth.google.com/web/>) was used to georeference specimens without coordinates based on the information present on the corresponding labels.

Ecological niche modeling

156 The occurrence records were reduced in number using spatial thinning, accomplished with the
 157 R package "spThin" (Aiello-Lammens et al. 2015), in order to create the ellipsoid niche model.
 158 To avoid issues associated with spatial autocorrelation, we maintained a minimum distance of
 159 10 km, considering the spatial resolution of the variables (~9.2 km at the equator) (Kramer-
 160 Schadt et al. 2013). This resulted in a final count of 270 records, following the methodology
 161 outlined by Cobos et al. (2018), which were used to calibrate and establish the final models.

162 Environmental data at a spatial resolution of 2.5 arc-minutes (~4.6 km at the equator) were
 163 obtained for this study from WorldClim (version 1.4, <http://www.worldclim.org>; Hijmans et
 164 al. 2005). WorldClim is based on interpolations of weather station data, encompassing monthly
 165 precipitation, minimum and maximum temperatures, from the period 1950–2000. Out of the
 166 19 available variables, four (mean temperature of wettest quarter, mean temperature of driest
 167 quarter, precipitation of warmest quarter, precipitation of coldest quarter) were excluded a
 168 priori due to known spatial inconsistencies between adjacent grid cells (Escobar et al. 2014;
 169 Campbell et al. 2015). Following the approach of Dey et al. (2021), we tested three different
 170 environmental sets to calculate the ellipsoid niche of *B. mendica*, aiming to avoid bias in
 171 characterizing the species niche centrality:

172 'Set 1' included all 15 variables.
 173 'Set 2' included only temperature-related variables.
 174 'Set 3' included only precipitation-related variables.

175 For each of these sets, we conducted a principal component analysis (PCA) using the
 176 'kuenm_rpca' function in the 'kuenm' package (Cobos et al. 2019) within RStudio 3.6.3 (R Core
 177 Team, 2021). The first three components, which collectively explained more than 90% of the
 178 total variance in the dataset, were retained for model calibration (see Table 1).

179 The models were constructed using the 'ellipsenm' package (Cobos et al. 2020), calibrated
 180 using the 95% pairwise confidence region for the ellipsoid, and evaluated using the
 181 'ellipsoid_calibration' function (Cobos et al. 2020). Two distinct methods were employed to
 182 create ellipsoid models:

183 'covmat,' which generates ellipsoids based on the centroid and a matrix of co-variances of the
 184 variables.
 185 'mvel,' which produces an ellipsoid that minimizes the volume without losing the data
 186 contained within (i.e., minimum volume ellipsoid; Van Aelst & Rousseeuw 2009).

Model selection was based on statistical significance (partial ROC; Peterson et al. 2008), while the proportion of testing data known to be in suitable areas and the prediction of unsuitable areas relied on omission rates ($E = 5\%$; Anderson et al. 2003) and prevalence (i.e., the proportion of space identified as suitable for the species; Cobos et al. 2020). The partial ROC metric was calculated using 500 bootstrap iterations, with 50% of testing data used in each iteration, and 5% testing data error due to uncertainty. Prevalence was calculated in both geographical and environmental spaces, considering only pixels with distinct combinations of all variable values (Cobos et al. 2020; Nuñez-Penichet et al. 2021).

The calibration area, which includes regions accessible to the species (Barve et al. 2011), featured a 50 km buffer from the occurrence records utilized in our models. The buffer size was determined based on observations of this species in its natural habitat, particularly males, which possess efficient wings and fly to locate females for mating.

Final parameters were selected based on the best-evaluated models and used to create the final models through ten replicates with bootstrapped subsamples, each comprising 75% of the data. These replicates were generated by excluding one occurrence record at a time. The ecological niche and suitability levels of *B. mendica* in geographical space were visualized, with binarization using a suitability threshold to exclude the 5% of data with the most extreme values. Visualization of results was carried out using QGIS v.3.10 (QGIS Development Team, 2020).

Phylogeographic analyses

Mesocoxal muscle tissue from 15 preserved *B. mendica* specimens was stored in 96 % ethanol. Genomic DNA was extracted using the E.N.Z.A.® Tissue DNA Kit protocol designed for animal tissue. We specifically targeted the barcoding region of the cytochrome c oxidase I (COI) gene, with a length of 658 base pairs, for amplification and sequencing. The primer sequences used were LepF1 (5'ATTCAACCAATCATAAAGATATTGG-3') and LepR1 (5'TAAACTTCTGGATGTCCAAAAAATCA-3'), as previously described by Hebert et al. (2004). Polymerase chain reaction (PCR) was conducted on a SENSQUEST Lab Cycler, with the following thermal conditions: initial denaturation at 95 °C for 5 minutes, followed by 38 cycles of denaturation at 95 °C for 30 seconds, annealing at 49 °C for 90 seconds, extension at 72 °C for 60 seconds, and a final extension at 68 °C for 30 minutes. Gel electrophoresis was used to confirm proper amplification and check for contaminations. The resulting PCR products were purified using Thermo Scientific Exonuclease I and the FastAP Thermosensitive

219 Alkaline Phosphatase Clean-up Kit. Sequencing was performed at MacroGen Europe, ensuring
220 adequate overlap with adjacent regions for sequence accuracy. Geneious R10
221 (<https://www.geneious.com>) was employed for nucleotide editing and contig assembly. A
222 multiple sequence alignment was carried out using Bioedit 7.2.5 (Hall, 1999) and was
223 subsequently converted into Fasta and Nexus formats for various analysis programs. All
224 sequences were deposited in GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) with the
225 following accession numbers: OR588779-OR588792. To visualize genetic relationships
226 between different geographic populations, a haplotype network was constructed using the TCS
227 network algorithm (Clement *et al.* 2002) as implemented in PopART v. 1.7.2 (Leigh and Bryant
228 2015).

229 For Bayesian analysis, the Akaike Information Criterion (AIC) implemented in jModelTest
230 v.2.1.10 was used to select the best-fitting DNA substitution models (Guindon and Gascuel
231 2003; Posada, 2008). The HKY model (Rodriguez *et al.* 1990) with a significant proportion of
232 invariant sites ($I = 0.7270$) (HKY + I) was identified by jModelTest as the best model and run
233 for 100,000,000 generations, sampling every 1000th generation. The first 10 % of generations
234 were discarded as burn-in. We used the remaining trees with average branch lengths to create
235 a 50 % majority-rule consensus tree with the sumt option of MrBayes. TRACER (Rambaut *et al.*
236 2018) was used to check that analyses reached an effective sample size (ESS) over 200 in
237 order to ensure correct chain convergence. Posterior probabilities (pp) were obtained for each
238 clade, where $pp \geq 0.95$ indicated significant support for clades. The run with the best log-
239 likelihood score was selected. Consensus trees were visualized and rooted with *Empusa*
240 *pennicornis* Pallas, 1773 as an outgroup in FigTree 1.4.2
241 (<http://tree.bio.ed.ac.uk/software/figtree/>), and edited using Inkscape vector graphics editors
242 (ver. 1.2). *Empusa pennicornis* was chosen as the outgroup because this genus belongs to the
243 same family (Empusidae).

244 Divergence time estimation was conducted using BEAST 2 v. 2.7.5 (Bouckaert *et al.* 2019).
245 We determined the substitution model by employing jModelTest version 2.1.10. The HKY
246 model with estimated base frequencies and gamma distribution (with 4 categories) was chosen.
247 Due to the unavailability of fossils for *Blepharopsis* or closely related genera, we calibrated
248 the tree using standard gene substitution rates, a method also employed in prior studies
249 (Papadopoulou *et al.* 2010; Wendt *et al.* 2022). Consequently, a clock rate of 0.0177 was
250 applied based on Papadopoulou *et al.* (2010). To explore the potential impact of different
251 models, we conducted two separate analyses utilizing Yule and Birth-Death tree priors. Each

Kommentiert [P9]: Fore what grou
may vary across organisms.

Kommentiert [P10]: Citation is mis

Kommentiert [P11]: Citation is mis

Kommentiert [P12]: Which used to
much faster evolving group with high
mantodeans.

analysis consisted of four independent Markov Chain Monte Carlo (MCMC) runs, each running for 50 million generations and sampling trees every 5,000 generations. After discarding the initial 10 % of trees as burn-in, we assessed convergence using Tracer version 1.7.1 (Rambaut *et al.* 2018). The final trees were combined using Tree Annotator v.1.10.4 and further edited using FigTree v.1.4.4 (<http://tree.bio.ed.ac.uk/>).

To explore the historical shifts in the geographical distribution of *B. mendica*, we employed two models for biogeographical range expansion: The Dispersal-Extinction-Cladogenesis (S-DEC) model and the Dispersal-Vicariance (S-DIVA) model, both implemented in RASP 4.3 (Yu *et al.* 2020). The input data for this analysis consisted of an ultrametric tree generated using BEAST v. 2.7.5. To enhance the precision of our analysis, we removed the outgroup from the tree using a feature provided by the RASP software.

We delineated seven geographical regions based on our knowledge of the current distribution of the species: (A) southern and central Iran, (B) Pakistan, (C) Lebanon, (D) Tunisia, (E) Morocco, (F) Canary Islands, and (G) Oman.

To account for uncertainties stemming from the tree's structure, we incorporated all trees sampled from BEAST analyses, excluding the initial 500 trees. In the S-DIVA analysis, we selected the "Allow Reconstruction" feature, which permitted a maximum of 100 reconstructions employing three random steps. Subsequently, we conducted up to 1,000 reconstructions to obtain the final tree. Each node in the analysis has attributed the potential for up to four distinct areas.

The results of the most suitable S-DIVA reconstructions were then summarized by utilizing the pruned maximum-clade-credibility tree derived from our Bayesian phylogenetic analysis. In the S-DEC analysis, we assumed equal probabilities of dispersal between areas, and all values in the dispersal constraint matrix were set to 1, considering four as the maximum number of areas.

Results

Field observations

Life cycle. Our research in the field indicates that *B. mendica* is an overwintering univoltine species. Thus, the nymphs emerge in summer (late July), as we have only found the first instar nymphs from late July to early August in their natural habitat, and they continue to grow throughout the season. Then, the larvae overwinter in the last instar (five records of living nymphs during winter from last week of October to first week of February) and become adults

Kommentiert [P13]: Somewhat ar
Egypt, a known distribution center fo

284 in spring (first sightings of adults; males first week of May; females second week of May).
285 Regarding oviposition, females began to lay their oothecae in June, as they often mate within
286 two weeks after reaching adulthood and typically lay their first ootheca within one week after
287 mating. However, it is important to note that oviposition timing can vary depending on various
288 factors such as temperature, humidity, and food availability. This trend has been observed
289 however with small differences in the distribution of this species from western North Africa to
290 the far Middle East.

291 **Ootheca.** Three oothecae of *B. mendica* were collected from branches of trees or bushes during
292 June and July 2020 (Figures 2d, e). They were already hatched when collected which could be
293 recognized by the presence of white eclosion sack-like structures in the emergence area. The
294 eggs in this species are arranged vertically in a row next to each other as was observed by
295 dissecting the field-collected oothecae dorsally (Fig. 2c).

296 **Defense behavior.** The first author observed two different responses to disturbance in this
297 species during field surveys. Either individual flew away when disruption happened, or they
298 extended their wings broadly and lifted their forelegs (Fig. 3a, b). Additionally, one female
299 made an odd menacing gesture (Fig. 3c).

300 **Habitat and hosting plants.** All individuals found in the field were encountered in more or
301 less xeric areas, with scarce vegetation composed of both herbaceous vegetation and spiny
302 bushes (Fig. 4). All specimens were found in Iran sitting on thorny bushes like *Prosopis* spec.
303 (Fig. 5a), *Alhagi* spec. (Fig. 5b), and *Astragalus* spec. (Fig. 5c), as well as *Tamarix* spec. (Fig.
304 5d). Similar vegetation patterns were observed also in Morocco and Tunisia (Fig. 5e and f).
305 Due to their coloring, *B. mendica* individuals are particularly suited for mimicking leaves, and
306 prickly or dry plants, i.e., the typical flora of semi-deserts.

307 **Laboratory breeding**

308 **Development of immatures and their color changes.** One ootheca was laid in the first week
309 of June by a female collected from the xeric shrublands of Bushehr province (N 27° 50' 37.3";
310 E 52° 03' 51.9"). This ootheca was 18 mm long, 12 mm high, and 6 mm wide (Fig. 2c). It had
311 a globular shape and, as mostly in this species, a very soft texture, completely covered with a
312 layer of spongy material, white in color at the time of laying (Fig. 2a). After one day, the
313 color turned into a creamy color. In total, 45 nymphs hatched from the ootheca's top rim after
314 five weeks (34 days, in the second week of May).

Kommentiert [P14]: Has stridulation this type of display? In my experience individuals of this species, stridulation

Kommentiert [P15]: So, no trees in

Kommentiert [P16]: A compilation this would be helpful.

315 Twenty-eight individuals (11 males, 17 females) of the 45 emerged nymphs completed their
316 life cycle. Twelve did not reach the second instar and died possibly due to poor molting. Five
317 died during the second and third instar. The time needed from hatching to adulthood on average
318 was 18 weeks (130 days) (Table 2). While most nymphs became adults after six (all males) or
319 seven molts (most females), four females required eight molts.

320 The first instar had a distinct color pattern on the thorax and legs, with mostly dark brown and
321 some white and black stripes (Fig. 1c). The color changed from light brown to creamy or white
322 from the second instar to subadult (Fig. 1d, e), and the adults' color ranged from bluish green
323 to grass green (Fig. 1a, b). We also observed color changes in adult specimens under laboratory
324 conditions. Thus, three adults first appeared ochre-brown or reddish, but after some days their
325 thoraxes became reddish, their wings greenish, and some other body parts reddish brown (Fig.
326 1a, b). The last larval instar had a longer lifespan than the others (Table 2). Overwintering of
327 nymphs explains the long duration of the last instar since it seems that the last instar nymph
328 will undergo a diapause process during winter (Table 2).

329 **Adult longevity.** The mean adult longevity of *B. mendica* at $25^{\circ}\text{C} \pm 2$ was 118 days (± 6 SD)
330 for females (range: 100–124 days), and 46 days (± 5 SD) for males (range: 39–55 days). SD
331 refers to standard deviation. The t-test recovered a statistically significant difference ($P <$
332 0.001) when comparing sexes (Suppl. Material Table S3). The average total life cycle was 216
333 days (± 9 SD) for females, and 132 days (± 7 SD) for males ($P < 0.27$) (Suppl. Material Table
334 S4).

335 **Oviposition.** To test for parthenogenesis, five of the 17 females who reached adulthood were
336 not mated. Three of these produced three unfertilized oothecae, none of which hatched. The 12
337 remaining females were joined with the males in a separate terrarium for mating. Eight females
338 successfully mated and produced a total of 11 oothecae, i.e., four laid one ootheca, two laid
339 two, and one laid three. Only four of these oothecae hatched.

340 There were no observable physical differences or deformations between the unfertilized,
341 unhatched, and hatched oothecae (Table 3). However, the number of eggs per ootheca varied
342 depending on the type and size of the ootheca (Table 3). The average number of eggs per
343 ootheca was higher in the hatched (mean: 43.7 ± 7.2 SD) and unhatched (mean: 31.8 ± 2.4 SD)
344 oothecae compared to the unfertilized ones (mean: 18.0 ± 2.9 SD) (Table 3). ANOVA tests
345 indicated significant differences among the three groups for all characteristics (i.e., weight,
346 length, width, and number of eggs), except for height. There is also a significant difference in

Kommentiert [P17]: Has the temp
unchanged during winter? If yes, the
be representative of the species lifespe
conditions, which is due to cool winte

weight and length between the hatched and unfertilized ootheca, as both Tukey p -values are less than 0.05, but there is no significant difference in height or number of eggs. Comparing hatched and unhatched oothecae revealed significant differences in weight, length, and number of eggs; however, there was no significant difference in width or height (Table 4).

Distribution and Ecological Niche Modelling

Blepharopsis mendica is largely associated with dry grasslands, ~~savanna-like habitats~~, and xeric shrublands from the Canary Islands to Pakistan (Fig. 6). Almost identical vegetation pattern was observed in Morocco and in Tunisia where this species has been observed in the wild. In Iran, where the distribution was poorly known prior to this study, it is also widely distributed, only excluding the driest regions in the central and eastern parts of the country and the high mountain areas in the west. The new records from Iran are listed in Supp. Information S1. The geographic projections of the ecological niche of *B. mendica* showed widespread climatic suitability across North Africa and southwestern Asia; lower suitability was recovered for the Sahel zone and southern Africa (Fig. 7, Supp. Information Fig. S1). The best fitting method to construct the climatic ellipsoids was ‘mve1’, with environmental set 1, containing principal components of all 15 variables; mean AUC, p -value of partial ROC, and omission rates were significantly better than random expectations ($P < 0.05$; Table 1). The prevalence of mean ellipsoidal models in geographical (G-space) and environmental (E-space) space was relatively high (0.912; Table 1). The complete report of ellipsoid characteristics (e.g., centroid, covariance matrix, semi-axes length, etc.) is given in Supp. Information S3.

Divergence dating, biogeography, and phylogenetic analyses

COI sequences of 15 specimens of *B. mendica* revealed 12 different haplotypes (Fig. 8). Bayesian tree and haplotype network analysis of *B. mendica* identified three distinct population groups: (i) Pakistan, (ii) Maghreb from Morocco to Tunisia, including the Canary Islands, and (iii) Middle Eastern populations from Lebanon, Oman, and Iran; the latter group is subdivided into a western subgroup (iiia) in Lebanon, Oman, and Khozestan (border Iran/Irak) and an eastern one (iiib) widespread in southern and central Iran (Fig. 9 and 10). Our biogeographic analysis using S-DIVA and S-DEC models revealed a divergence of the lineage in Pakistan from the ancestor of the other groups about 1.5 million years ago. Another vicariance event separated the Maghreb populations from the remaining ones about 1.3 Mya. Less than 1 Mya, a dispersion event led to the split between the Middle East (Lebanon, Oman, Khozestan) and

Kommentiert [P18]: The records a from India, Somalia and most parts of suggest a more thorough search through literature (e.g. papers by Chopard, U

Kommentiert [P19]: This result suggests the exclusion of Egypt and neighboring regions, the exclusion of Somalia and neighboring regions is important in order to assess whether the Egyptian populations are related to those in Lebanon, Maghreb, and (2) the populations south of Sudan etc.) are related to the ones from the Arabian Peninsula, which could also have implications for the validity of *B. mendica nuda*. A greater search has been missed here.

378 most other Iranian populations (Fig. 9). Hence, historical events, including vicariance and
379 dispersion, played pivotal roles in shaping the genetic pattern of *B. mendica* populations.

380 Discussion

381 Life cycle and variability in nymphal development

382 The life cycle of mantids is divided into two phases: the developmental period from hatching
383 to reaching adulthood and the reproductive period as adults, which is defined by adult
384 longevity. Korsakoff (1934) recorded nine instars for females and eight instars for males of *B.*
385 *mendica* from hatching to adulthood. In our study, nymphs only passed through fewer instars,
386 i.e., six for males and seven (rarely eight) for females, which is similar to *Hierodula* species,
387 which pass through six to nine instars to reach adulthood (Leong, 2009; Raut *et al.* 2014;
388 Mirzaee *et al.* 2022a). The variability in the number of instars in mantids might be due to
389 different factors, such as temperature, resource availability and quality, humidity, genetics, sex,
390 and photoperiod (Esperk *et al.* 2007). Therefore, a higher temperature, humidity, and resource
391 availability and quality in our study might decrease the number of molts in this species. The
392 higher temperatures used to rear the nymphs of *B. mendica* in our study (33–35 °C), in
393 comparison to Korsakoff's study (27 °C), could have accelerated the developmental rate of the
394 specimens, resulting in fewer instars being needed to reach adulthood. Similarly, if the quality
395 and availability of food were different between the two studies, this could have also influenced
396 the developmental rate and the number of instars required for the mantids to reach adulthood.
397 In Korsakoff's study specimens were fed by rose moth caterpillars but in our study, we used
398 mealworms, flies, and grasshoppers. Additionally, differences in the genetic background and
399 sex of the mantids used in the two studies could also have contributed to the differences in the
400 number of instars e.g., the mantids used in this study were from Iran and the mantids Korsakoff
401 used in his study were from North Africa.

402 As in our study, Maxwell (2014a) also observed a similar variation in the number of instars in
403 *Stagmomantis limbata* bred in captivity, with 64 % of nymphs requiring six, and 36 % requiring
404 seven instars. He considered this variation in the number of instars as a "bet-hedging" strategy
405 used by females to produce variation in development among siblings (Maxwell, 2014b). It thus
406 might be a survival strategy, for mantid species in general and for such species living in extreme
407 and often largely unpredictable habitats like *B. mendica* in particular, because sisters hatching
408 together will enter the reproductive phase at different points in time. This is increasing the

Kommentiert [P20]: Of course, his
shaped the genetic pattern observed
does not say much, if no theories of v
originated through dispersal and wha
proposed.

Kommentiert [P21]: Please state v
were from.

Kommentiert [P22]: Rather random
that the two taxa are not closely relat
with *Idolomantis* and *Empusa*, genera
available.

Kommentiert [P23]: This is good. C
(1964).

Kommentiert [P24]: This informati
above.

409 chance that at least some females are reproductive in a suitable time window, hence
410 safeguarding the survival of regional populations of the respective species.

411 Adaptations of the incubation time of oothecae, and nymphal overwintering

412 The incubation duration of oothecae in Mantodea often is species-specific, but can also be
413 influenced by the environment. Therefore, it is important to consider the impact of
414 environmental conditions when studying the developmental biology of any species
415 (Greyvenstein *et al.* 2022). It seems that temperature, particularly daily maximum temperature,
416 is the key factor for hatching in different mantid species such as *A. spallanzania* (Rossi, 1792)
417 (Battiston & Galliani 2011). Various mantis species employ distinct strategies for
418 overwintering and development, demonstrating their ability to adapt to diverse environmental
419 conditions. These differences may be influenced by specific genetic factors, potentially
420 resulting in different life cycles even when multiple species share the same habitat.
421 Overwintering strategies in Mantodea can be different between different genera but little
422 information regarding these strategies is available for this group of insects. Some Mantidae
423 genera, for example, *Miomantis* Saussure, 1870, *Hierodula* Burmeister, 1838 and *Mantis*
424 Linneus, 1758, go into a facultative diapause phase during the ootheca stage (Ramsay, 1984;
425 Mirzaee *et al.* 2022a). However, some other species in different genera like *Ameles* Burmeister,
426 1838, *Empusa* Illiger, 1798, and *Severinia* Finot, 1902, have the strategy to overwinter as
427 nymphs (Battiston & Galliani 2011; Shcherbakov & Govorov 2021). In our study, the last
428 nymphal instar of *B. mendica* lasts longer than the previous ones (as shown in Table 2). This
429 developmental pattern is also seen as an adaptation strategy to survive overwintering as a
430 nymph.

431 In our study, the average incubation period for oothecae of *B. mendica* was 36.8 days (\pm 2.9
432 SD). This is similar to other members of the Mantidae family, such as *Hierodula tenuidentata*
433 Saussure, 1869 (35.1 days), *Orthodera ministralis* (30.9 days), and *Hierodula ventralis* (25
434 days) (Suckling, 1984; Raut *et al.* 2014; Mirzaee *et al.* 2022). However, shorter (e.g., 16 days
435 for *Ephestiasula pictipes*; Hymenopodidae) and much longer incubation periods (e.g., 142–209
436 days for *Stagmomantis limbata*; Mantidae) also exist (Robert, 1937; Vanitha *et al.* 2016).
437 Therefore, the adaptation strategy for the incubation period can vary across different species.
438 Even among species with similar incubation periods, the strategies used can be different. For
439 instance, females of *Hierodula transcaucasica* species lay their oothecae in late autumn, which
440 then undergoes a dormant process during winter, and egg development begins when

Kommentiert [P25]: *Miomantis* da
Mantidae.

Kommentiert [P26]: For *Mantis*, se
Schwarz et al. 2017.

Kommentiert [P27]: Only southern
Northern ones overwinter as ootheca

Kommentiert [P28]: Again, why on
compare with other empusids as well

Kommentiert [P29]: Please add m
comparison.

Kommentiert [P30]: Please note th
species are tropical and subtropical a
oothecae.

hat formatiert: Schriftart: Kursiv

441 temperatures become suitable; the same also applies to *Mantis religiosa* and *Sphodromantis*
442 *viridis* (Kaltenbach 1963, Berg et al. 2011, Mirzaee et al. 2022a, Raut and Gaikwad 2016). On
443 the other hand, females of *B. mendica* and *Empusa* spp. lay their ootheca in spring so that it is
444 the nymphs that have an overwintering strategy.

hat formatiert: Schriftart: Nicht K

hat formatiert: Schriftart: Kursiv

445 Having a short incubation time for the ootheca seems to be an appropriate strategy in wet
446 tropical areas without distinct seasonal variation. In contrast, temperate species require longer
447 incubation periods or even dormancy, especially when the egg is in the overwintering stage.
448 For species living in regions with an arid summer and a mild winter climate, an intermediate
449 incubation time might be the most suitable adaptation. This is because egg maturation takes
450 place during the hottest and driest time of the year when there is limited food supply. Then, the
451 larvae hatch with the first autumn rains, and reproduction in the following year will end when
452 the living conditions become unfavorable (Robert, 1937; Vanitha et al. 2016; Raut and
453 Gaikwad 2016; Mirzaee et al. 2022a).

Kommentiert [P31]: This is not the
species from dry areas also employ th
reason is that in submediterranean a
the winters are too cold to overwinte
oothecae can survive there the winte
overwintering is the older strategy, si
tropical regions with a dry season. Or
oothecae adapted to the cold or able
could colonize northern habitats.

454 **Color polymorphisms and variability as an adaptive defense mechanism**

455 Coloration can be influenced by genetic factors and environmental conditions (Okay, 1953;
456 James, 1944). The different colors of different instars and the color changes of *B. mendica*
457 therefore might be interpreted as an adaptational defense according to the respective
458 environmental conditions and the ability of the species to camouflage and thus avoid predators.
459 A similar developmental strategy was also observed for *Mantis religiosa* often changing its
460 color from brownish to green along its larval development (Battiston and Fontana 2010). Under
461 artificial conditions, some adult brown *M. religiosa* females showed an incomplete but clearly
462 visible variation toward green tones in some body parts, even when no green components were
463 available in the cages. Even more, *B. mendica* is able to change its color in the adult stage
464 without using the renovation processes of a molt. This latter phenomenon is also known for
465 *Miomantis caffra* (Ramsay, 1990) and *M. religiosa* (Okay, 1953); the mechanisms behind are
466 still unknown.

Kommentiert [P32]: See Berg et al
analysis of this phenomenon.

467 **Characteristics of ootheca and parasitization**

468 Various factors, including male presence, temperature, humidity, food availability, and
469 genetics, affect the size, color, and structure of oothecae (Robert, 1937; Breland and Dobson
470 1947; Hurd et al. 1995). Mantid oothecae are consumed by certain beetles (*Orphinus* spp.
471 *Attagenus* spec. *Phradonoma* spec.; Dermestidae) and parasitized by wasps (*Podagrion* spp.;
472 Torymidae) (Kershaw, 1910; Hawkeswood, 2003; Bolu and Ozaslan 2015, Mirzaee et al.

Kommentiert [P33]: There are ma
Rielia, *Anastatus*, *Podagrionella*. Plea

2021b, 2022b). These factors have a significant impact on not only the appearance of oothecae but also their survival rates and hatching, and therefore the population dynamics of mantids in their natural habitats. Korsakoff (1934) discovered that the chalcidoid wasp *Podag~~r~~ion* spec. parasitized the oothecae of *B. mendica* that he collected from North Africa, with more parasitoids than *B. mendica* nymphs emerging. In our study, none of the oothecae were parasitized due to laboratory conditions, but further research is necessary to identify the species of beetles or wasps preying or parasitizing on *B. mendica* oothecae in the wild.

Distribution and ecological biogeography

Our climate suitability model recovered suitable areas that well reflect the known distribution of *B. mendica* (Figs. 7 and 8), ranging from the Maghreb in the west to the Middle East as far east as Pakistan and the driest parts of western India. Hence, high climatic suitability was exclusively recovered in hot and dry regions (Supp. Information Figure. S1). A recent study conducted by Nasser *et al.* (2021) analyzing *B. mendica* in Egypt equally found that temperature-related variables but also low altitude were the factors most significantly contributing to the climatic niche model. In their study in contrast to our work, however, precipitation-related variables had a relatively small influence.

In contrast to our climate models, however, major climatically suitable areas, particularly in northern Libya (Supp. Information Figure. S1), represent a geographic gap within the known distribution extending to both sides. As this part of Libya is generally hot and dry, and the prevailing vegetation features may favor the occurrence of *B. mendica* (Ageena, 2013), we argue whether this distribution gap is real or not because it just might be due to sampling deficits. A similar gap of knowledge regarding the species' distribution applies to Saudi Arabia, where high climatic suitability levels were also recovered. Therefore, further fieldwork is needed in these two regions to clarify this aspect.

However, a real geographic split into two major groups is also possible, one Maghreb group, largely distributed in north-western Africa, and one group around the Arabian Peninsula, ranging from Egypt via Israel, Iraq, and Iran to Yemen, but avoiding the driest inner parts of the peninsula. The formation of these two distinct geographic groups in *B. mendica* might be the result of a combination of historical and extant environmental factors shaping the distribution and genetic makeup of the species over time. Thus, these two groups originating from one common ancestral population might have been separated by a physical barrier, such as temporally existing stretches of extreme desert in northern Libya, preventing gene flow

Kommentiert [P34]: Because their uniform in term of precipitation.

Kommentiert [P35]: Really? Why is there than in the South?

Kommentiert [P36]: Or incomplete

Kommentiert [P37]: What about K (1991)?

Kommentiert [P38]: This theory so the Figures 8 and 9 and suffers from a samples. What about Pakistan and In

Kommentiert [P39]: 3? 4?

Kommentiert [P40]: Extreme desert occurrence of the species as long as o are available. Please check more liter of this species in N Africa.

Also, northern Libya might actually be species due to more extensive vegeta

among these groups. Over time, genetic differences might have accumulated through genetic drift or natural selection, leading to the formation of two distinct gene pools. Environmental factors, such as differences in climate and vegetation (Mulligan *et al.* 2017), also might have played a role in shaping the distribution of *B. mendica*. For example, the drier parts of the Arabian Peninsula may not provide suitable habitats for the species, whereas the more humid areas around its coastlines as well as the southern Maghreb region may provide more favorable conditions.

Kommentiert [P41]: But are there

Suitable climatic conditions were also recovered in parts of southern Africa. Thus far, however, the true absence of *B. mendica* in this region might be due to the interspersed, geographically rather large regions whose climatic conditions permanently have been completely unsuitable (i.e., tropical forests of central and eastern Africa; Supp. Information Figure. S1), in combination with the limited dispersal capability of *B. mendica*.

Kommentiert [P42]: Southern Mag should it be different from Egypt or s Note that the species is absent (for n Africa north of the Atlas Mountains, v Mediterranean climate.

Despite some known occurrences in the Sahel zone, our model recovered only marginally suitable climatic conditions for this region. However, a Google Maps search revealed that one of the recorded locations is a truck parking lot in Sudan. It consequently is likely that the observed *B. mendica* specimen was accidentally transported there by truck, as studies have indicated that, similar to other insects, praying mantids, including their egg cases (i.e. oothecae), are frequently introduced to new areas through transportation, including railways and other commercial routes (Battiston *et al.* 2020). The two further specimens collected in southern parts of Chad and Niger are suspicious and need future confirmation. Consequently, three possibilities exist for these Sahel zone records: (1) They are wrong or represent displaced individuals; (2) the species is very rare in this zone offering it only marginal living conditions; (3) the species is frequent in the Sahel zone and the conditions are suitable, but the region is completely understudied for this species. Further studies in the Sahel region are therefore necessary to resolve this open question.

Kommentiert [P43]: Again, please The species naturally occurs there.

Kommentiert [P44]: Why suspicious

Kommentiert [P45]: Please re-work doing a proper literature search.

The only major region where *B. mendica* was frequently observed in areas not indicated as suitable by our model is the mountainous parts of northern Iran. We believe that this is due to the complex climatic structuring of this area with very heterogeneous microclimatic conditions (Heshmati, 2007). The hot and dry conditions needed by *B. mendica* are mostly restricted to relatively small pockets in the landscape, such as deep valleys, so the species is occurring rather locally. As the climate in most parts of these landscapes is unsuitable for *B. mendica* at the grit level, our model likely was unable to detect these small-scale pocket-like occurrences. This

537 model confirms the general conservation assessment of this species (Battiston, 2016) which
538 hypothesized the existence of diminutive and fragmented local populations within the extensive
539 distribution range of *B. mendica*.

Kommentiert [P46]: As in oasis all
Saudi-Arabia.

540 Divergence dating and phylogeographic analyses

541 Our study also provides insights into the evolutionary and biogeographic history of *B. mendica*.
542 The distinct genetic lineages identified in Pakistan, north-western Africa (Morocco, Tunisia,
543 Canary Islands), the Middle East (Lebanon, Oman, Iran-Iraq border, most likely Egypt), and
544 Iran (south and central regions) reflect the species' ability to adapt to and to survive in different
545 geographical with different environmental conditions (Figs 9 and 10).

Kommentiert [P47]: I think the wh
conditions are very similar despite th

546 The separation of *B. mendica* from other Empusid mantids might have occurred around 2.5
547 mya suggesting that this species has evolved independently from other Empusid mantids all
548 along the Pleistocene. The subsequent divergence of the Pakistan lineage from the remaining
549 populations around 1.5 mya may have been influenced by geographic barriers or environmental
550 changes, maybe going along with the general aridification alongside the mid-Pleistocene
551 Transition (1.2–0.8 mya), hence causing vicariance (Thunell, 1979; Bertoldi *et al.* 1989,
552 Berends *et al.* 2021).

Kommentiert [P48]: First, the conf
is too vast to allow such a narrow win
time. It could as well be around 4 my
other species more closely related to
Empusa, such as *Blepharodes* (a Sahe
(E Africa) and *Gongylus* (SE Asia). The
respective clades might shed another
than that proposed here.

For empusid phylogeny see Wieland
Roy (2019).

553 The separation of the Maghreb lineage a little later, i.e., around 1.3 mya, likely also resulted
554 from vicariance that again could have been triggered by the mid-Pleistocene Transition's
555 aridification (Berends *et al.* 2021), maybe making the territory of today-Libya hostile for the
556 species due to extreme dryness, indicating that climate-driven geographical isolation might
557 have played an important role in the differentiation of *B. mendica*. Less than one mya and hence
558 at the end of the mid-Pleistocene Transition, a dispersal event out of Iran (detected by our
559 RASP analysis) was responsible for the colonization of the Arabian Peninsula or the Middle
560 East with subsequent vicariance and differentiation among these three regions. The arid
561 Pleistocene conditions in the Maghreb region prevailing during most of the last 0.5 my might
562 also be responsible for vicariance between its eastern and western regions for *B. mendica*
563 assumed 360.000 years ago, an often-observed fact in this region, but mostly with considerably
564 higher vicariance age (Husemann *et al.* 2014). The colonization of the Canary Islands is a rather
565 recent event dated by our molecular clock to 80,000 years before the present, and hence
566 immediately before the true onset of the Würm glaciation (Ampferer, 1925).

Kommentiert [P49]: I would rather
dispersal event following the aridifica
species prefers desert and semi-dese
implies that a once vast area was frag
doubtful given the moister conditions
Pleistocene transition proposed here

Kommentiert [P50]: Why should d
a species adapted to arid regions? Th
suffers from a premature assumption
not occur in Libya, which is erroneou
be caused by the type of data used, d
period when Libya has been rarely vis
Older literature might shed an unbiase
supposed "distribution gap" presume
authors. I propose to check the distri
(which can depend on water other th
precipitation) across the Libyan Sahar
coastal hills, as well as a proper litera
further pursuing this theory.

Kommentiert [P51]: Why should b
responsible for the divergence? Isn't
the humid periods ("green Sahara") o
arid refugia?

567

568 **Conclusion**

569 This study adds information on the little-known desert mantid species *B. mendica*, including
570 its life cycle, ootheca (egg case), defense behavior, and preferred habitat. Additionally, our
571 climate suitability model provided important insights into the species' distribution,
572 corroborating existing records while also pointing out areas where sampling has been limited
573 and regions that still remain unexplored. However, to fully understand the distribution patterns
574 with its underlying phylogeographical structures and the factors shaping the ecological niche
575 of *B. mendica* across different geographical regions, further research, fieldwork, and
576 validations are essential. These efforts will contribute to a more comprehensive understanding
577 of the species distribution and its relationship with environmental factors.

578 **Acknowledgments**

579 We wish to express our sincere appreciation to Christoffer Fägerström, curator at Lund
580 Museum of Zoology, Sweden, Peters Ralph, curator at Zoological Research Museum
581 Alexander Koenig, Germany (ZFMK), and Alexander Riedel, curator at State Museum of
582 Natural History Karlsruhe, Germany (SMNK), for generously providing us with invaluable
583 coordinates and data. Additionally, we would like to express our gratitude to Oscar Maioglio
584 (World Biodiversity Association, WBA, Italy), Evgeny Shcherbakov (Lomonosov Moscow
585 State University, Russia), and Valeriy Govorov (Charles University, Prague, Czech Republic)
586 for providing the legs of the samples collected from Canary Islands, Fasa, Fars, Iran and Oman.
587 We would also like to thank Hossein Abdollahi for his aid during fieldwork, and Shiraz
588 University Genetic lab for providing *Drosophila melanogaster* in order to feed first instar
589 nymphs.

590 **Conflicts of Interest:** The authors declare no conflict of interest.

591 **References**

- 592 Adair, E.W. (1924) On parthenogenesis in *Miomantis savigny* Saussure. *Bulletin de la Société*
593 *Entomologique d'Égypte*, 8, 104–148.
- 594 Ageena, I. (2013) Trends and patterns in the climate of Libya (1945-2010). Doctoral
595 dissertation, University of Liverpool.

596 Ampferer, O. (1925) Uⁿber Wachstumsunterschiede zwischen Fern- und Nahgletschern. *Die*
597 *Eiszeit*, 2, 41–49.

598 Battiston, R. Amerini, R. Di Pietro, W. Guariento, L.A. Bolognin, L. and Moretto, E. (2020) A
599 new alien mantis in Italy: is the Indochina mantis *Hierodula patellifera* chasing the train for
600 Europe? *Biodiversity Data Journal*, 88, e50779. <https://doi.org/10.3897/BDJ.8.e50779>.

601 Battiston, R. and Galliani, C. (2011) On the life-cycle of *Ameles spallanzania* (Rossi, 1792)
602 (Insecta, Mantodea). *Natural History Sciences*, 152(1), 25–35.
603 <https://doi.org/10.4081/nhs.2011.25>.

604 Battiston, R. Picciau, L. Fontana, P. and Marshall, J. (2010) *The Mantids of the Euro-*
605 *Mediterranean Area*. World Biodiversity Association, Verona. pp. 240.

606 Battiston, R. Fontana, P. (2010) Color change and habitat preferences in *Mantis religiosa*.
607 *Bulletin of Insectology*, 63(1), 85–89.

608 Bolu, H. Ozaslan, C. (2015) *Mantis religiosa* L. (Mantodea: Mantidae) a new host for
609 *Podagrion pachymerum* Walker (Hymenoptera: Torymidae) in Turkey. *Agriculture &*
610 *Forestry*, 61, 183–187. <https://doi.org/10.17707/agricultforest.61.2.16>.

611 Brannoch, S.K. Wieland, F. Rivera, J. Klass, K. Bethoux, O. and Svenson, G.J. (2017) Manual
612 of praying mantis morphology, nomenclature and practices (Insecta, Mantodea). *ZooKeys*, 696,
613 1–100. <https://doi.org/10.3897/zookeys.696.12542>.

614 Berends, C.J. Köhler, P. Lourens, L.J. van de Wal, R.S.W. (2021) On the cause of the mid-
615 Pleistocene transition. *Reviews of Geophysics*, 59, e2020RG000727. [https://doi.](https://doi.org/10.1029/2020RG000727)
616 [org/10.1029/2020RG000727](https://doi.org/10.1029/2020RG000727)

617 Breland, O. and Dobson, J. (1947) Specificity of mantid ootheca (Orthoptera: Mantodea).
618 *Annals of the Entomological Society of America*, 40, 557–575.
619 <https://doi.org/10.1093/aesa/40.4.557>.

620 Bertoldi, R. Rio, D. and Thunell, R. (1989) Pliocene-Pleistocene vegetational and climatic
621 evolution of the south-central Mediterranean. *Palaeogeography, Palaeoclimatology,*
622 *Palaeoecology*, 72, 263–275.

623 Caesar, M. Roy, R. Legendre, F. Grandcolas, P. and Pellens, R. (2015). Catalogue of
624 Dictyoptera from Syria and neighbouring countries (Lebanon, Turkey, Iraq, and Jordan).
625 *Zootaxa*, 3948(1), 71–92. <https://doi.org/10.11646/zootaxa.3948.1.5>.

626 Cukier, M. Guerrero, G.A. and Maggese, M.C. (1979) Parthenogenesis in *Coptopteryx viridis*,
627 Giglio Tos (1915) (Dictyoptera, Mantidae). *The Biological Bulletin*, 157, 445–452.
628 <https://doi.org/10.2307/1541029>.

629 Ehrmann, R. (2011) Mantodea from Turkey and Cyprus (Dictyoptera: Mantodea). *Articulata*,
630 26(1), 1–42.

631 Esperk, T. Tammaru, and T. Nylin, R. (2007) Intraspecific variability in number of larval
632 instars in insects. *Journal of Economic Entomology*, 100, 627–645.
633 <https://doi.org/10.1093/jee/100.3.627>.

634 Greyvenstein, B. Du Plessis, H. Moulin, N. and Van den Berg, J. (2020) Distribution of
635 *Galepsus* spp. in Southern Africa and life history of *Galepsus lenticularis* (Mantodea:
636 Tarachodidae). *Insects*, 11(2), 119. <https://doi.org/10.3390/insects11020119>.

637 Greyvenstein, B. Du Plessis, H. and Van den Berg, J. (2022) Notes on the lifecycle and
638 distribution of *Sphodromantis gastrica* (Stål, 1858) (Mantodea: Mantidae) in South Africa.
639 *African Entomology*, 30(1). <http://dx.doi.org/10.17159/2254-8854/2022/a13967>.

640 Hawkeswood, T.J. (2003) Notes on the biology and food items of three Australian Dermestidae
641 (Coleoptera). *Calodema*, 1, 1–4.

642 Heshmati, G.A. (2007) Vegetation characteristics of four ecological zones of Iran. *International*
643 *Journal of plant production*, 1(2), 25–224. <https://doi.org/10.22069/IJPP.2012.538>.

644 Hurd, L.E. Eisenberg, R.M. Moran, M.D. Rooney, T.P. Gangloff, W.J. and Case, V.M. (1995)
645 Time, temperature, and food as determinants of population persistence in the temperate mantid
646 *Tenodera sinensis* (Mantodea: Mantidae). *Environmental Entomology*, 24, 348–353.
647 <https://doi.org/10.1093/ee/24.2.348>.

648 Husemann, M. Schmitt, T. Zachos, F.E. Ulrich, W. and Habel, J.C. (2014) Palaeartic
649 biogeography revisited: Evidence for the existence of a North African refugium for western
650 Palaeartic biota. *Journal of Biogeography*, 41, 81–94. <https://doi.org/10.1111/jbi.12180>.

651 James, H.G. (1944) Color changes in *Mantis religiosa* L. *The Canadian Entomologist*, 76(6),
652 113–116.

653 Kershaw, J.C. (1910) The formation of the ootheca of a Chinese mantis, *Hierodula saussuri*.
654 *Psyche*, 17, 136–141. <https://doi.org/10.1155/1910/78374>.

655 Korsakoff, M.N. (1934) Contribution à l'étude du *Blepharopsis mendica* Fab. *Revue d'Écologie*
656 (*La Terre et La Vie*), 4(5), 272–276.

657 Korsakoff, M.N. (1935) Contribution à l'étude du *Blepharopsis* Fabr. (suite). *Revue*
658 *d'Ecologie, Terre et Vie, Société nationale de protection de la nature*, 120-124.

659 Leong, T.M. (2009) Oviposition and hatching in the praying mantis, *Hierodula patellifera*
660 (Serville) in Singapore (Mantodea: Mantidae: Paramantinae). *Nature in Singapore*, 2, 55–61.

661 Maxwell, M. (2014a) Developmental patterns in *Stagmomantis limbata* (Mantodea: Mantidae):
662 Variation in instar number, growth, and body size. *Journal of Orthoptera Research*, 23, 49–58.
663 <https://doi.org/10.1665/034.023.0104>.

664 Maxwell, M. (2014b) A synoptic review of the genus *Stagmomantis* (Mantodea: Mantidae).
665 *Zootaxa*, 3765, 501–525. <https://doi.org/10.11646/zootaxa.3765.6.1>.

666 Mirzaee, Z. and Sadeghi, S. (2019) On a summer collection of mantids (Insecta: Mantodea)
667 from Lorestan province with nine new records. *Iranian Journal of Animal Biosystematics*,
668 15(2), 175–187. <https://doi.org/10.22067/ijab.v15i2.79314>.

669 Mirzaee, Z. and Sadeghi, S. (2021) A survey on mantids fauna (Insecta: Mantodea) from Fars
670 Province. *1st Fars Biodiversity Conference*, 1, 25.

671 Mirzaee, Z. Lotfalizadeh, and H. Sadeghi, S. (2021b) Chalcidoid parasitoids (Hymenoptera:
672 Torymidae and Eupelmidae) of mantids (Mantodea) oothecae in Iran. *Phytoparasitica*, 50,
673 487–499. <https://doi.org/10.1007/s12600-021-00965-1>.

674 Mirzaee, Z. Sadeghi, S. and Battiston, R. (2022) Biology and Life Cycle of the Praying Mantid
675 *Hierodula tenuidentata* Saussure, 1869 (Insecta: Mantodea). *Iranian Journal of Science and*
676 *Technology, Transaction A: Science*, 46, 1163–1169 [https://doi.org/10.1007/s40995-022-](https://doi.org/10.1007/s40995-022-01325-2)
677 01325-2.

678 Mirzaee, Z. Sadeghi, S. Háva, J. Battiston, R. and Ruzzier, E. (2022b) New observations of
679 Coleoptera associated with Mantodea ootheca and an overview of the previous records. *Bulletin*
680 *of Insectology*, 75(2), 223–230.

681 Mulligan, M. Keulertz, M. and McKee, M. (2017) Environmental Factors in the MENA
682 Region: A SWOT Analysis. CIDOB.

683 Nasser, M. Okely, M. Nasif, O. Alharbi, S. GadAllah, S. Al-Obaid, S. Enan, R. Bala, M. and
684 Al-Ashaal, S. (2021) Spatio-temporal analysis of Egyptian flower mantis *Blepharopsis*
685 *mendica* (order: Mantodea), with notes of its future status under climate change. *Saudi Journal*
686 *of Biological Sciences*, 28(4), 2049–2055. <https://doi.org/10.1016/j.sjbs.2021.01.027>.

687 Okay, S. (1953) Formation of green pigment and color changes in Orthoptera. *Bulletin of*
688 *Entomological Research*, 44(2), 299–315. <https://doi.org/10.1017/S0007485300023099>.

689 Panhwar, W.A. Tasleem, S. Asif, M. Alam, M. Anwar, F. Nisa, Z.U. *et al.* (2020) Praying
690 mantis (Mantodea: Dictyoptera) of Pakistan: A review-based study. *Bulletin of Environment,*
691 *Pharmacology and Life Sciences*, 9, 180–183.

692 Ramsay, G.W. (1990) Mantodea (Insecta), with a review of aspects of functional morphology
693 and biology. *Fauna of New Zealand*, 19. <https://doi.org/10.7931/J2/FNZ.19>.

694 Raut, G.A. Bhawane, G.P. and Gaikwad, S.M. (2014) Laboratory studies on the life history of
695 *Hierodula ventralis* Giglio-Tos, 1912 (Mantodea: Mantidae). *Journal of Entomology and*
696 *Zoology Studies*, 6, 147–152.

697 Raut, G.A. and Gaikwad, S.M. (2016) Observations on the Life cycle, mating and cannibalism
698 of *Mantis religiosa religiosa* Linnaeus, 1758 (Insecta: Mantodea: Mantidae). *Journal of*
699 *Entomology and Zoology Studies*, 4(6), 478–482.

700 Robert, R.A. (1937) Biology of the Bordered mantid, *Stagmomantis limbata* Hahn (Orthoptera,
701 Mantidae). *Annals of the Entomological Society of America*, 30, 97–109.

702 Shcherbakov, E. and Govorov, V. (2021) Riders on the storm? A short note on the biology of
703 *Severinia turcomaniae* (Saussure, 1872) (Mantodea: Toxoderidae). *Annales de la Société*
704 *entomologique de France* (N.S.), 57,4, 372–378,
705 <https://doi.org/10.1080/00379271.2021.1950050>.

706 Suckling, D.M. (1984) Laboratory studies on the praying mantis *Orthodera ministralis*
707 (Mantodea: Mantidae). *New Zealand Entomologist*, 8(1), 96–101.
708 <https://doi.org/10.1080/00779962.1984.9722478>.

709 Thunell, R.C. (1979) Climatic evolution of the Mediterranean Sea during the last 5.0 million
710 years. *Sedimentary Geology*, 23(1-4), 67–79.

- 711 Vanitha, K. Bhat, P.S. Raviprasad, T.N. and Srikumar, K.K. (2016) Biology and behaviour of
712 *Ephestiasula pictipes* (Wood Mason) (Hymenopodidae: Mantodea) under captive breeding.
713 *International Journal of Pest Management*, 62, 308–318.
- 714 Walker, L.A. and Howell, I.G. (2016) Sexual cannibalism in a facultative parthenogen: The
715 springbok mantis (*Miomantis caffra*). *Behavioral Ecology*, 27, 851–856.
- 716 Zehzad, B. Kiabi, H. and Madjnoonian, H. (2002) The natural areas and landscape of Iran: an
717 overview. *Zoology in the Middle East*, 26,1, 7–10.
718 <https://doi.org/10.1080/09397140.2002.10637915>.